THE ORIGIN OF THE ELECTRICITY TISSUES IN FISHES[1]

PROFESSOR ULRIC DAHLGREN

PRINCETON UNIVERSITY

AMONG the many specializations of animal tissues four are so fundamental in nature and so specific in their function that they stand out as exceptionally favorable objects for study, particularly as to their origin and evolution. These tissues are those which produce motion, heat, light and electricity in quantities, and for the benefit of the entire organism.

Of these, motion is the most important. Without the power to move it is probable that few animals would be able to survive and to evolve to any great degree of specialization. Thus the forms which did not develop organs of motion at an early period or those which lost it subsequently would be eliminated and would leave all other and higher degrees of specialization to be attained by such animals as had developed or retained muscle tissue.

Heat production was probably an important factor in the development of many land forms, especially in regions of the earth that became subject to cold, and the possession of any small part of this power would tell to a marked degree in the favorable selection of its possessor.

[1] Lecture delivered before the Society of American Naturalists in Boston on December 29, 1909. A fuller technical account with illustrations of the histogenesis of the electric tissue in *Gymnarchus* will shortly appear in another journal.

Of the other two abilities, that to produce light and to generate electricity, we find that both are rare. Luminosity is found to be widely distributed among the various kinds of animals, most of the principal groups having one or more representatives which can produce light. And yet this is, after all, a rare specialization and the percentage of animals which are luminous is very small indeed. It is not so absolutely necessary as the power to move nor can it be regarded as having the selective value that the possession of heat-producing tissues must have. Its real function, sexual, warning, or for purposes of seeing objects in the dark, has not been satisfactorily determined for any groups except possibly the deep-sea fishes and even here we find more to be without it than with it.

As to the last of the dynamic tissues, that which produces electricity, we have here a tissue which is remarkable to an extreme degree both for the rarity of its occurrence and its narrow distribution, is being confined to one group of vertebrates, the fishes, and found here among only seven families.

In these seven groups the tissue seems to have developed absolutely independently and to have formed seven separate types of organ differing markedly from one another in details of structure and position of the organ and yet all adapted, through certain analogous developments, to perform the same function.

We evidently have here a tissue of comparatively recent origin, phylogenetically, and one of the first studies to be made toward a knowledge of its evolution is to find out what can be learned from its history in the individual or its histogenesis.

Of the seven types of organs two are found in elasmobranchs and the remaining five in teleost fishes. The histogenesis of the two elasmobranch forms has been worked out by Ewart, Engelmann, Babuchin, Ogneff and others, but the corresponding history of this tissue in the teleosts has remained unproved with the exception of one form, *Gymnarchus*, the ontogenetic origin of whose electric organ the writer presents below.

Before explaining the histogenesis of the electric tissue in this teleost fish a brief résumé of what is known of the development of the two elasmobranch types of electric tissue should be given.

In the young embryos of *Raja*, Ewart and Engelmann found that the position of the future electric organ was occupied by well-developed muscle in no way different from the other muscle tissue of the trunk. In the half-developed fish the transformation of certain of these single muscle fibers into single electroplaxes was observed to begin, at a later period in those skates which had the simpler types of tissue, at an earlier time in those which had the more highly developed types. This change in the muscle fiber consisted of a widening of its anterior end, which finally resulted in the formation of a flat plate lying at right angles to the position of the former muscle fiber. The posterior end of the fiber degenerated, forming in some cases a useless tail-like appendage in other cases atrophying altogether.

During this change the myo-fibril bundles assumed various curved positions and formed the thick " striated " layer of the electroplax, while the larger part of the cytoplasm formed a flat anterior layer or "electric layer" as well as a thick covering, the nutritive layer, on the posterior surface. This posterior layer was produced into more or less developed papillæ. The nuclei multiplied by amitotic division and were segregated into the anterior and posterior layers, those in the anterior or electric layer forming a very regular layer themselves. The nerve supply, consisting of several medullated fibers, approached the anterior or electric surface and, dividing into very many fine naked branches, terminated in as many disc-shaped plates in this surface.

In the torpedoes, or electric rays, Ogneff has worked out the histogenesis and found that, as in the other elasmobranch forms (the skates), each electroplax develops from one muscle cell. But there are several important differences. The adult organ is a far more highly specialized structure in *Torpedo* than in *Raja* and the muscle cell is

still in a very young stage, a mere myo-blast possessing but one nucleus, at the time it begins to change. It is the end furthest from the electric surface or negative pole of the future electroplax that begins to enlarge first into a club-shaped form and then into a disc which continues to expand laterally and grow thinner until it becomes an exceedingly thin plate. The nucleus of the young myoblast or electroblast divides by amitosis into many nuclei, which are distributed through the plate and the nerve supply is large and ends in tiny discs that cover the whole upper, negative or " electric " surface.

In *Gymnarchus,* the only teleost whose histogenesis is known, the electroplaxes of the adult fish are arranged in eight long cylindrical masses, four on each side, and embedded in the muscle of the tail. Each cylinder consists of a row of the thick electroplaxes spaced apart by about their own length of the jelly-like " electric connective tissue" usually found in these organs. Each electroplax conforms to the outline of the cylinder laterally and is bounded anteriorly and posteriorly by surfaces from which a few short blunt papillæ emerge. The electroplax consists of a central core of a fibrillar nature, the fibrils being arranged in the form of approximate layers and giving the appearance of a transverse striation of this region. As will be seen below, this striation does not represent the striation of the voluntary muscle of vertebrates.

This core is covered by a layer of undifferentiated cytoplasm of moderate thickness which contains the numerous nuclei of the syncytium. The nuclei are arranged in a single layer, but, since the central core does not extend into the majority of the papillæ, the nuclei form a central mass in these appendages.

The nerve supply consists of several large medullated fibers which approach each electroplax from the rear and are easily seen to end on its posterior surface. Each of the naked ultimate branches terminates in a knobbed end plate which is imbedded in the substance of the outer

layer both on the papillæ and on the posterior surface itself.

The whole cylinder, both electroplaxes and electric connective tissue, is separated from the surrounding muscle tissue by a connective tissue sheath in which a few isolated pigment cells are to be seen. The electroplaxes do not exactly correspond in the adult either to the myotomes or to the vertebræ.

The significant development of the electric tissue takes place between the ninth day of embryonic life, at which time the embryo contains unchanged muscle tissue in its tail, and the 40-day embryo which possesses the organs in practically its adult condition. The critical changes take place within even closer limits; from the 11th day to the 15th would include them. The stages used in this examination were but four in number, the ninth, eleventh, twelfth and fortieth, four out of the seven valuable embryos given the writer by Dr. Arthur Shipley, Dr. Richard Assheton and Dr. J. Graham Kerr, to whom many thanks are due. This material was collected by Mr. John Samuel Budgett in Africa, he most unfortunately losing his life from fever shortly afterwards.

The ninth-day embryo shows no trace of any electric tissue. The myotomes, as shown in a longitudinal section are very regularly formed and are composed at this time of many perfect muscle fibers with the myofibrils developed in several bundles in the peripheral cytoplasm. These muscle fibers are all parallel with one another and with the long axis of the body. Connective tissue is but little developed although it is found sparingly between the muscle fibers.

In the embryo of eleven days the electric tissue has begun to form. Eight regions in each muscle segment, each region composed of a few (10–40) of the young muscle fibers, have become prominent through the slightly greater density of their cytoplasm and the beginning degeneration of the muscle cells which immediately surround them. These eight regions in each myotome lie directly in front of and behind eight corresponding

regions in the myotomes before and to the rear of them. They thus mark out anterio-posterior lines which represent the location of the future cylinders. The young muscle fibers composing them retain their myofibril bundles unchanged and the striation of these fibrils is exactly like that of all the other myofibrils in other muscle fibers. The multiplication of nuclei goes on by amitosis as in the regular muscle cells.

The next stages examined are seen in an embryo whose age was between twelve and fourteen days. The word "stages" is used because in such an embryo quite a range of developmental steps can be found, owing to the fact that the tail is still extending and consequently the anterior electroplaxes are older than the posterior. This condition is reversed in the adult, for here it can be seen that the posterior electroplaxes advance further in size and degree of specialization than the anterior ones did. A young stage in this embryo shows that the groups of cells in each myotome which are forming the electroplaxes have become so closely approximated that they form a larger syncytium composed of the several smaller syncytia or muscle fibers which went to form it. This mass has assumed a rather distinct, elongate, spindle-shaped form and each one has increased in length so as to overlap its neighbor both ahead and behind it by a third or more of its length. The myofibrils show a tendency to occupy the central core of the young electroplax and are still striated. In this stage the nerve supply can be seen approaching the spindle from somewhat behind its middle and coming in contact with it at about the junction of its middle and posterior thirds.

The older electroplaxes in this same stage show a change. This change consists in a segregation of the myofibrils in the central core of the mass, where they still run parallel with each other and in a straight anterior-posterior direction; except in the now swollen middle third of the structure where they have assumed a wave-like direction. Furthermore, they have lost the larger part of their striation, this feature being retained only in

either end of the fibrils. The less differentiated cytoplasm has become segregated into a peripheral layer and, owing to the more rapid growth in length of the entire body than of the individual electroplaxes, these latter have become drawn apart and no longer overlap as they did at an earlier date.

Before proceeding further a word is necessary as to the fate of the surrounding muscle fibers and the way in which the electroplaxes become marked off from the surrounding tissues.

At first the muscle cells that will be transformed into electric tissue are in direct contact with the surrounding muscle cells of the myotome. Then these immediately surrounding fibers begin to degenerate by a peculiar process of hystolysis that strangely enough resembles somewhat the formation of an electroplax. The middle of the fiber swells up and the myofibrils lose their striation; lastly the ends are drawn in, the nuclei fragment and the whole mass becomes a lump of amorphous matter that finally disappears.

The next developmental changes in the electroplax can perhaps be best described by comparing the stage last described with the practically adult electroplax. In this we find that the middle third of the young form has expanded into the cylindrical body of the completed stage. The two end portions have failed to grow in size and have become one of the several blunt papillæ that have evaginated from both ends. This comparative atrophy of the posterior end of the spindle has left the nerve ending on the posterior surface of the electroplax and on the evagination that project from it, while the anterior end is in contact with a considerable development of capillary blood channels that lie in the electric connective tissue.

Most interesting in this older stage is the fate of the myofibrils. They have lost their striation completely, the dark staining anisotropic substance seeming to have dissolved and left well-defined fibrils of the isotropic substance alone. These fibrils no longer lie so evenly together although still associated in groups. The wave-like

direction that they had previously assumed has increased until they now run back and forth at right angles to the axis of the electroplax and consequently in the same relation to their former course. This gives the striated appearance which might be taken for the degenerated remains of the real muscle striation that the developing electroplax formerly possessed.

We thus can see that, while the electroplax of *Raja* and of *Torpedo* were formed from single muscle cells, in the first case by a widening of the negative or electric end and in the second instance by a widening of the positive or nutritive end, the electroplax of *Gymnarchus* is formed by the association of several myoblasts into a single syncytium and the widening of the middle part of this structure into the electroplax.

The other anatomical features of *Gymnarchus* which have caused it to be classed with the *Mormyridæ* demand that a comparison of this organ be made with the apparently widely different organ found in the various mormyrus groups. That found in *Mormyrus Oxyrynchus* will serve as a type and its general plan has been well shown by Ogneff and Schlichter. Here it is evident that a number of consecutive and entire myotomes have been converted into electroplaxes and that the middle layer of each electroplax is composed of unaltered and clearly striated myofibril bundles. The large number of these fibril bundles and their distribution indicate that the whole electroplax is a syncytium composed of all or most of the cells which would otherwise have gone to make up the single myotome. In this we find an agreement with the electroplax of *Gymnarchus* which is also formed from several cells. In the one case all the cells in the myotome have been used; in the latter only those lying in eight particular localities.

Further homology is seen in the disposition of the probably superfluous myofibrils. In both forms they are relegated to a middle position in the electroplax while the apparently more important cytoplasm forms layers on the anterior and posterior surfaces of the structure. Also, in both, the now useless myofibril bundles are

packed out of the way at right angles to the axis of the electroplax which remains the same as the former axis of the muscle cells that were used to form it.

The only difference lies in the fact that the striation of the fibrils is retained in the *Mormyrus* forms while it is lost in *Gymnarchus,* the dark-staining anisotropic substance apparently dissolving away.

From what little can be predicted concerning the possible origin of the electric tissue in the other teleost forms it is probable that the Mormyridæ (including *Gymnarchus*) are the only fish in which the electroplax is formed as a syncytium from more than one cell.   In *Astroscopus, Electrophorus* (forming *Gymnotus*) and *Malopterurus* the structures show every evidence of having been developed from single myoblasts with the exception of *Malopterurus,* where it is a question as to whether they are not evolved from gland cells instead.

The evolution of these structures was most probably not based upon a natural selective basis.   It is true that all muscle cells produce a slight static discharge at the moment of contraction, and that the far greater shock given by the electroplax is possibly a development of this same discharge.   But Darwin in his " Origin of Species " has already said that the electric organs of fishes were one of the serious obstacles in the way of his natural selection theory, showing that the very slight discharge of the more primitive organs could not possibly have been useful to their possessors to the extent of an excluding selection based on their presence or degree of development.

Some good evidence as to the methods of evolution ought to be deduced from the degree of specialization and distribution of electric organs in some of the groups; even if experimental work seems at present to be impossible.   In the skates, for instance, we find a very even and general distribution of an organ and tissue that is apparently in course of evolution, but which has not yet arrived at a state of efficiency.   It seems that the organ must have originated in the common ancestor of the thirty or more species of skates found in the seas of the world.

All the Rajidæ have this organ and yet their close allies show no sign of its appearance. One form in particular was formerly classed with the skates, but some years ago was removed on anatomical evidences from this group by D. S. Jordon and classed in another genus. The writer dissected a specimen of this species with great interest and care and found that there was no trace of electric tissue. And yet this species is undoubtedly closely related to the skates and must have inherited at least their potential powers to develop electric tissue. Furthermore this species is skate-like to an extreme degree in form and habit and must have lived under conditions and surroundings similar to those which we must assume were the ones, if any, that stimulated the skate ancestors to change muscle tissue into electric tissue. Evidently there are internal as well as external conditions and stimulæ to be taken into account.

Likewise among the torpedoes; all possess a very highly developed organ, evidently a common inheritance from some ancestor in which it originated. Subsequent variation in the tissue has not kept pace with the fair amount of external variation in the several species. It seems that the impulse to evolve this tissue has extended into all the members of these two groups, a real inner stimulus working independently of outer condition.

On the other hand, other groups of similar form, appearance and mode of life to some of the other electric fishes absolutely lack the electric tissues. These may or may not be nearly related. A rather remarkable example is to be seen in *Astroscopus* and its related form *Uranascopus scaber*. These two fish look so much alike that one may be used to show the fishermen what the other looks like. Their habits are practically the same. Also this feature is noticeable among the Gymnotidæ, whose various members show many grades of specialization but have not been sufficiently studied as to the possession of rudimentary electric organs. These studies together with the histogenesis of other teleost electric tissues, particularly that of *Malopterurus,* are most attractive fields for future work.

THE MATERIAL BASIS OF MENDELIAN PHENOMENA [1]

DR. REGINALD R. GATES

MISSOURI BOTANICAL GARDENS, ST. LOUIS, MO.

SINCE the rediscovery of Mendel's results at the beginning of the century, a very extensive and important field of hereditary phenomena has been actively developed, and the conceptions and explanations of Mendelian behavior have been changing with great rapidity. Many explanations and views of the phenomena of dominance, recessivity, latency and segregation have been proposed, and the only conception of Mendel which has remained essentially unmodified by Mendelians is that of the purity or unity of the characters in the gametes. Even this conception has been viewed by various workers in many lights, with a more or less complete and sweeping denial of an actual segregation of characters in the germ cells.

In the time at my disposal I shall bring before you the results of only one *Œnothera* cross, which shows Mendelian behavior in certain characters, and in the discussion of these results shall point out certain modifications of our conceptions of Mendelian segregation which they necessitate.

The cross in question is *Œnothera nanella* × *O. biennis, O. nanella* being a mutant from *O. Lamarckiana* and the *O. biennis* in the cross being from a wild race growing around the New York Botanical Garden. The seeds were first obtained from Dr. D. T. MacDougal. In the F_1 of this cross two types were produced, evidently corresponding to DeVries's twin hybrids. One of these types breeds true in the second generation and is the same as the type obtained in the F_1 of *O. Lamarckiana* × *O. biennis.* The other is a new type, with unexpected

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[1] This paper was presented before the American Society of Naturalists in Boston, Mass., December 29, 1909.

characters, which I have called *O. rubricalyx*. None of
the peculiar characters of either parent are present in
this hybrid. But this is not so remarkable, because
crosses between the *Œnothera* mutants frequently lose
the distinctive marks of both parents and give *O. La-
marckiana*. The same form, *O. rubricalyx*, has appeared
in my cultures as a mutant or extreme variant from *O.
rubrinervis,* from which it differs only in possessing a
red hypanthium instead of green, a marked increase in
the red color pattern of the sepals (the median ridge of
the sepals being also red instead of green), and in the
production of a conspicuous quantity of red pigment on
the *under* surface of the petioles of the rosette leaves, as
well as in other parts of the plant. The type can there-
fore easily be recognized by observing the under surface
of the rosettes, and in the flowering stage the conspicuous
deep red buds render the plant very attractive and showy,
distinguishable from *O. rubrinervis* at a glance. It dif-
fers from *O. rubrinervis* in its greatly increased capacity
for anthocyanin production, a difference which expresses
itself in nearly every organ of the plant. A full illus-
trated account of this cross will be published elsewhere.

In the F_2 this type splits in the Mendelian ratio of
3:1, giving approximately 75 per cent. *O. rubricalyx* and
25 per cent. *O. rubrinervis*. I have not yet bred the
later generations, but the *O. rubrinervis* may be expected
to breed true and the *O. rubricalyx* to split as before.

In this single cross there are many facts which throw
interesting side lights on the nature of Mendelian be-
havior. In the first place, only one character splits in
Mendelian fashion, the others remaining true. Hence,
if proof of this proposition were needed, here we have
proof that Mendelian phenomena are not universal, even
in the forms in which they occur. The *O. rubricalyx*
which appeared as a mutant from *O. rubrinervis* also
splits in the same manner, a certain number of the off-
spring reverting to the *rubrinervis* condition, though I
have not been able to determine whether this is a Men-
delian ratio. These and other facts make it very prob-

able that the explanation of Mendelian phenomena is to
be sought in the nature of the character itself, which
conditions and perhaps determines this type of in-
heritance.

Another important point in connection with this hybrid
is that the split in the F_2 does not produce a return to
the condition of one of the grandparents, as in typical
Mendelian behavior, but the difference between the two
types of the F_2—*O. rubricalyx* and *O. rubrinervis*—is a
purely quantitative difference, in capacity for pigment
production, although morphologically this difference is
expressed in certain very definite regions of the plant.
There are no intermediates between these two types,
each being an independent condition of stability.   The
difference, therefore, clearly dates back to the germ cells.

That a quantitative difference between germ cells in
their capacity for pigment production can behave in
Mendelian fashion, showing the phenomena of dominance
and segregation, is of fundamental significance in the
interpretation of the nature and material basis of these
phenomena.

Riddle ('09) has brought together in an interesting
way the facts of physiology and biochemistry which show
that the various pigment colors in mammals and other
animals are different stages in the oxidation of a single
melanin pigment by the enzyme tyrosinase. In the light
of the facts of quantitative Mendelian inheritance which
I have presented, it is clear that color inheritance in
the mammals can also be most easily interpreted as a
case of quantitative inheritance, due to initial quantita-
tive differences of some sort in the germ cells themselves.
It is not impossible that nearly all Mendelian inheritance
may be found, on sufficient analysis of the characters, to
be of this sort.   Studies in variation show that many
apparently qualitative differences, when analyzed, are
found to be purely quantitative in origin.   It should be
remembered in the case of melanin pigments, as Riddle
also points out, that while some tyrosin oxidations lead
to the formation of melanins, others result in the usual

waste products, such as carbon dioxide and ammonia. Of course, only the former can be of significance in inheritance, and it is probable that whatever determines in how far the former process of tyrosin oxidation shall take place, will be found to control or determine these quantitative differences in the end-products of the germ cells.

It is interesting and suggestive to note in this connection that Morgan ('09) has adopted a quantitative interpretation of the sex-determining factors in the germ cells of insects and other organisms.

It is important to enquire what is the nature and origin of this quantitative difference, such as must occur in the germ cells of the hybrids I have described. It is most reasonable to suppose that it originates at the time the germ cells are formed, *i. e.*, during the reduction divisions, for the whole individual from a very early stage of the seedling to mature development shows one or the other of the alternative characters. Hence, the germinal difference must date back to the fertilized egg, and if this be true we must logically take it back farther still, on account of the definite Mendelian proportions, to the individual germ cells which united in fertilization, and hence probably to the reduction divisions.

The question of the relation of the chromosomes to Mendelian behavior has been so often discussed that I will only touch upon it here, to point out that the theory of qualitative hereditary differences among the chromosomes is not incompatible with the view that differential Mendelian characters are properties of the germ cell as a whole. If, during the reduction division, certain of the chromosomes which are segregated into separate cells are chemically unlike, then different groupings will arise and the whole germ cells whose nuclei the different groups enter will soon experience the effect of those differences, and accordingly such germ cells would be expected to become unlike as a whole. This follows necessarily, not only from the continual active inter-

changes in metabolism between nucleus and cytoplasm, but from the unity of the cell, which modern biology has abundantly proved. Hence there is no difficulty in supposing that differences which must be thought of as characterizing the germ cell as a whole, originated from chromosomal differences during reduction. On the other hand, there seems no necessity for assuming that *all* germinal differences originate in the chromosomes, although if they originated in the cytoplasm it is necessary to assume as a *vera causa* either a separation of cytoplasmic substances during reduction, of which we have no visible evidence, and which seems unlikely for various reasons, or *quantitative* cytoplasmic differences in the cells of a tetrad. The quantitative difference which must exist between the germ cells of *O. rubricalyx* and *O. rubrinervis* may possibly be conceived of as originating in the cytoplasm and then becoming a property of the germ cell as a whole.

It is even possible that this is not a difference in amount of matter of any sort, but rather in the energy-content of the two types of germ cell, although we have no means of knowing how or why such a marked difference in energy-content should arise.

To attempt to account for the manner of origin of a *O. rubricalyx* mutant from a *O. rubrinervis* germ cell would at the present time be purely speculation. De-Vries' conception of a new unit becoming suddenly activated in the germ plasm seems too formal an assumption to be accorded the dignity of an explanation. The fact that the *O. rubricalyx* mutant reverts to *O. rubrinervis* may be looked upon as evidence in favor of his view that a mutant originates as a hybrid, from the union of a mutated with a non-mutated germ cell.

I should also point out that the origin of *O. rubricalyx* from *O. rubrinervis* may perhaps be significant as indicating an orthogenetic tendency to an increase of pigment production, although this increase has taken place by definite germinal steps, particularly in the origin of *O. rubricalyx* from *O. rubrinervis*.

The significance of the fact that I have succeeded in producing *O. rubrinervis* as one of the types resulting from this cross, is too obvious to require pointing out. In the light of these facts, it is not impossible that other mutants can be similarly synthesized.

Much experimental work has been directed to the study of the physiology of anthocyanin production in the plant. Without entering into the details of this work it may be said that two general theories of anthocyanin production have been developed. E. Overton ('99), Mirande ('07), Molliard ('07) and others conclude that it arises from an accumulation of sugars in the cell sap, which unite with tannic acid to produce a glucoside. Overton showed experimentally that low temperature and high light intensity both cause anthocyan production. Mirande ('07) called attention to the development of red in leaves eaten by insects;[2] and Combes ('09a) produces the same result by annular decortication. In every case the result is interpreted as due to an accumulation of sugars. J. Laborde ('08), from his experiments deduced a slightly different view, namely that formaldehyde or one of its polymerization products may cause tannin transformation, to produce color. Further, Overton, Laurent, Molliard and others, found that various seed plants grown in sugar solution show a marked increase in anthocyan production, which indicated clearly a relation, direct or indirect, between the presence of sugars and the development of anthocyan. Whether such an increase in anthocyan production is inherited is not known, but presumably it would not be inherited. Of course, many variations in pigment production are of a nonheritable sort, but it is equally certain that in *O. rubri-*

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[2] In this connection I may call attention to certain observations of my own upon the effects of the attacks of a certain insect on the buds of *Œnothera*. The very young buds are stung by this insect and such buds undergo several characteristic changes in development. The hypanthium fails to develop and the base of the cone becomes very thick. In *O. Lamarckiana* (and the same is true at least of several mutants) there is also always a conspicuous amount of red developed on the sepals under these circumstances, but the buds of *O. biennis*, while they undergo the same morphological changes, never develop any red.

calyx the increased pigment production is a heritable character, and therefore the change which brought it about must have been of a fundamental sort, in the germ plasm.

A more recently developed hypothesis of anthocyan formation, suggested by Pick in 1883 and supported by the work of Palladin ('08), Buscalioni and Pollacci ('04), in their extensive memoir, and others, is that anthocyan originates from the action of oxydases upon the respiratory chromogens of the cell, the latter being aromatic bodies which on oxidation yield colored compounds. The experiments of Molliard ('09) support the latter theory by showing the necessity for the presence of oxygen in anthocyan production. Molliard also showed that, when grown in a sugar solution, the respiratory exchanges of plants are more intense.

Combes ('09*b*) has recently harmonized the two theories. He shows that there is a close relation between the production of anthocyan and an increase in the proportion of sugars and glucosides in the cell sap. He concludes that since the formation of anthocyan, a compound of glucoside nature, is correlative with an increase of the total glucosides, the anthocyan cannot be formed from preexistent glucosides, but from some other source; and since there is also an increase in chromogens (Palladin) therefore anthocyan is not derived from chromogens already existing, but its formation must be provoked by the accumulation of sugars, which increases the respiratory exchanges and appears to determine the acceleration of oxidation processes. Under these conditions the production of glucosides is increased, and these are, in part at least, anthocyanins.[1]

It is scarcely necessary to point out that, whatever may be the chemistry and physiology of anthocyanin production, in the case of *Œnothera rubricalyx* there must have been a fundamental change in the germ plasm by reason of which, under the same external conditions as *O. rubri-*

[1] See also the important recent papers of Miss M. Wheldale. Proc. Roy. Soc. London B, 81: 41–60. P··c. Cambridge Phil. Soc. 15: 137–168 and Reports to the Evolution Committee of the Royal Society, V., pp. 26–31, 1909.

nervis, it reacts with much greater pigment production; a reaction which shows itself with great definiteness in the buds and the rosette leaves.

Although plants and animals equally exhibit Mendelian phenomena, yet the part of the organism which must be looked upon as constituting the germ plasm, and hence the basis of such phenomena, shows several important differences in Metazoa and Metaphyta, two of which may be pointed out.   Most important of these differences is probably the absence of a *Keimbahn* in plants, in the sense in which it is known to be present in many animals. The classical cases of *Ascaris* (Boveri) and *Cyclops* (Häcker) need only be cited.   More recently, other work, such as that of Hegner ('09) in the Coleoptera, has shown that the germ cells are formed from certain free nuclei, at an early stage in the segmentation of the egg.   Thus set aside, they rest and undergo very few divisions, until a late stage of embryonic life.   There is no evidence whatever of a similar process in higher plants, and it is probably made impossible by the method of plant growth. On the other hand, it may be pointed out that while, in plants, there are no resting cells set aside in the body tissues, to serve later as reproductive cells, yet a lineage of cells exists, which may be looked upon as a *Keimbahn* in one sense.   Every one who has studied plant embryos recognizes their characteristically large nuclei with huge nucleoli having a large chromatin content.   A similar appearance is characteristic of all undifferentiated meristematic cells, so that such cells, forming a lineage from the egg cell to the spore mother cells, may be thought of as constituting a *Keimbahn* for the plant, though evidently in a somewhat different sense from that in which the term is employed for animals.   The fact that in such a lineage, a great number of cell generations intervene between the fertilized egg and the spore mother cell, together with the fact that the meristematic cells forming this lineage are near the surface of the plant, where they are almost directly exposed to environmental influences (and not hidden away in the in-

terior of the body as in animals), doubtless accounts for the greater plasticity exhibited by plants. Indeed, it is a matter for wonder that, under these conditions, plants show such hereditary constancy. The accurate reproduction, generation after generation, of the most minute hereditary differences, shows the relative fixity of the material of the germ plasm.

The work of the Marchals ('06 and '07) with the mosses seems to show clearly that, during the meiotic divisions of spore formation, an actual segregation of sex-producing tendencies or elements takes place. Much other evidence of a similar sort in plants might be cited if time permitted, and the case of the sex chromosomes in insects is too well known to require more than mention. But while the reduction divisions seem the most natural place to look for an explanation of the Mendelian proportions, yet on the other hand there is much evidence that the phenomena of "splitting" also occur at other times in the life history. Bateson ('05) has shown that in two races of sweet peas (*Lathyrus odoratus*), one of which has long pollen grains and the other round, the long pollen character is dominant in the F_1. If a segregation of characters took place here during the reduction divisions, we should find 50 per cent. of each type of pollen grain. But plants having long pollen give only long, or they may give three plants with long pollen to one with round. Only in "very rare and exceptional" cases is there a mixture of long and round in the same plant, and in such cases they are found only in certain flowers of an individual. Rosenberg ('06) found that in the hybrid *Drosera longifolia* $\times$ *D. rotundifolia,* in some cases two pollen grains of a tetrad resemble each parent, the grains differing chiefly in size. More recently, however, he has found ('09) that the variations in the size of the hybrid pollen grains probably depend upon the numbers of chromosomes which enter the respective daughter nuclei during reduction, and hence this difference in pollen grains will no longer serve as evidence for a segregation of characters at this time.

There is nothing to indicate that the phenomena of

vegetative splitting, or reversion to the parental types, in such forms as the reputed graft-hybrid, *Cytisus Adami,* differ in any essential respect from Mendelian segregation in germ cells.   In angiosperms, the great majority of which are hermaphrodite, there is a separation of tendencies, which may be thought of as a "segregation," in the Anlage of every flower, the stamens producing microspores and male gametophytes, while the ovules bear the megaspores, which develop the female gametophyte.   These two tendencies—namely, for the stamens to produce microspores and the ovules to produce the female gametophyte—are almost never interchanged (although Němec, '98, has described a case in *Hyacinthus,* in which the microspores may produce a structure resembling more or less the female gametophyte).   Whether there is here a separation of substances in the cytoplasm or chromoplasm during the division of certain cells in the Anlage of the flower, is not known, but it is not impossible that such is the case.

Viewed from this standpoint, all differentiation during ontogeny may be considered a "segregation."   A consideration of what this really consists in would involve the whole great problem of individual development, which I shall not touch upon here.   But it may be pointed out that maturation, particularly in Mendelian hybrids, may be looked upon as a period of active germ cell differentiation.

The factors involved in such differentiation may be, in some cases, quite as complex as those involved in development itself, but as I have shown from the evidence of these *Œnothera* hybrids, and as appears from color inheritance in mammals and from other evidence, in many cases at least the difference between Mendelian germ cells must be of a simple quantitative sort, involving either a difference in the amount of certain material substances or a difference in the energy-content of certain constituents.

From this point of view, many instances of Mendelian behavior are seen to be cases of quantitative inheritance.

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MENDELIAN PHENOMENA WITHOUT
DE VRIESIAN THEORY[1]

DR. W. J. SPILLMAN

U. S. DEPT. OF AGRICULTURE

THAT the phenomena of Mendelian segregation of character pairs is inextricably linked with the de Vriesian notion of pangenes is an opinion widely held, both by the advocates of the theory of discontinuous variation and by the opponents of that theory. Professor S. J. Holmes was one of the first American biologists to point out the fallacy of this idea.[2] He called attention to the fact that due consideration of the phenomena reported by Mendelian investigators did not lead to the theory of discontinuous variation as a necessary consequence.

While in the present paper it is my purpose to present an explanation of Mendelian phenomena without resorting to the idea of unit characters, I do not wish to be understood as belittling the important work done by de Vries and his followers. While contending that the de Vriesian doctrine that organisms are aggregates of separately heritable characters is unsound, I believe this investigator has uncovered a new type of variation which must be reckoned with as *a* means of evolution, not by any means the sole, or even the most important, means. For want of space, I am compelled, in what follows, to present some opinions without submitting all the evidence in favor of them. However, an attempt will be made later to present this evidence more fully. It seems to the writer that what Darwin considered to be fluctuating variations, amenable to the action of natural selection, may now be regarded as consisting of four distinct types of variation. First, we have those variations in the progeny of a given individual, or pair of individuals, which are due to what we may call "Mendelian recombination of characters."

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[1] This paper was presented before the American Society of Naturalists, in Boston, Mass., December 29, 1909.

[2] See AMER. NAT., May, 1909.

Natural selection may have a very important influence on variations of this kind, since the variations are hereditary. The recognition of variations of this type must of course be attributed to Mendel, but de Vries, Correns, Von Tschermak and perhaps some others must be recognized as rediscoverers of this principle.

In the second place, after we have eliminated all variation caused by Mendelian recombination we still have a type of variation which is more and more coming to be called fluctuation, and which is due wholly to environment. Such variations are now believed not to be hereditary and therefore not amenable to the action of natural selection. In this connection we need only mention the important investigations of Johanssen on beans and barley,[3] the work of Nilssen and his able staff at Svalöf on wheat, oats and other species, and the recent classic work of Jennings on *Paramecium*.[4] The work of these investigators indicates strongly that selection is without effect on fluctuations due to environment. Dr. E. M. East, in Illinois Experiment Station Bulletin No. 127, reaches the conclusion that no effect of selection has been proven in clonal varieties of potatoes.

In the third place, de Vries found a type of variation which the cytological work of Gates,[5] Rosenberg[6] and Gager,[7] indicates to be due to irregularity in the distribution of chromosomes in mitosis.

Gates has shown that in the species with which de Vries worked there are irregularities in chromosome distribution. Furthermore, de Vries has shown that his mutants differ from each other in almost every detail, just as we should expect them to do if each of the chromosomes is more or less responsible for the whole process of development.

[3] W. Johannsen, " Ueber Erblichkeit in Populationen u. Reinen Linien," Jena, Fisher, 1903; Rep. 3d Int. Con. on Genetics, pp. 98–113.

[4] H. S. Jennings, *Proc. Amer. Phil. Soc.*, XLVII, No. 190, 1908; *Jour. Exp. Zool.*, Vol. 594, June, 1908.

[5] R. R. Gates, *Science*, January 31, 1908; *Science*, February 12, 1909, and elsewhere.

[6] O. Rosenberg, Rep. 3d Int. Con. on Genetics, pp. 289–291.

[7] E. Stewart Gager, Publications of New York Botanical Garden.

Rosenberg has shown that the irregularity of certain first-generation *Hieracium* hybrids is accompanied by irregularity in the number of chromosomes present.

Quite recently Gager, in his study of the effect of radium emanations on plants, has not only produced mutants apparently of the character of those found by de Vries, but has shown that in mitosis in treated specimens there is irregularity in the distribution of chromosomes. The writer some time ago suggested a similar explanation for the interesting work of McDougall in which mutants were produced by chemical stimulants. The behavior of the Rubus hybrid produced by Burbank, and resulting in the *Primus* berry, is so closely parallel to that of *Hieracium* hybrids studied by Rosenberg that a similar explanation at once suggests itself.

Boveri's classic work on the relation of chromosomes to development strongly supports the view that the de Vriesian mutants are due to loss or exchange of chromosomes, and this view is consistent with the work of Wilson, Morgan, Stevens and others on the relation of the chromosomes to sex.

I think, therefore, that we are in position to recognize, at least tentatively, a new type of variation, which is due to irregularities in the distribution of chromosomes, and which I shall call "de Vriesian mutation." These variations, being hereditary, are amenable to the action of natural selection, and must therefore be recognized as one method of evolution. In a certain sense these mutations are discontinuous, and the reason for this is apparently clear.

When we consider all the facts in the case, which I have not time here to outline, I think that few biologists will contend that all evolutionary changes are due to Mendelian recombination, or to de Vriesian mutation as defined above. The enormous diversity in groups having the same number of chromosomes, as well as observable differences in the chromosomes themselves, render any such view untenable. I therefore postulate a fourth kind of variation due to fundamental changes in what we may

call the germ plasm, and I am inclined to believe that this
is by far the most important type of evolutionary change.
Whether changes of this character are continuous or dis-
continuous is not a very important question. It is more
important to ascertain their cause and nature. I imagine
they are largely chemical changes in the composition of,
or changes in the relative amounts of substances present
in, the germ plasm. If these changes are continuous the
work of Johannsen, Nilssen, Jennings and East, above
referred to, indicates that they are very slow. Such
changes are certainly hereditary, and are thus a factor,
and I believe the most important factor, in evolution.

One point regarding fundamental changes in the germ
plasm it is important to remember: a gradual change
might go on for a long time in the chemical activity of the
cell before reaching a point where any outward manifesta-
tion of this change would appear. For instance; in some
purple flowers there is reason to believe that the color is
due to some such action as that of acids and alkalies upon
the color of litmus, the flower being red or purple accord-
ing to the amount of some substance present. Now a
gradual change might go on in the relations between the
substances concerned without producing any visible effect
until a certain point is reached, when a marked effect is
produced, giving what appears to be a discontinuous
change, but what may be in reality a critical point in a
slow and gradual change.

Riddle, in his recent very interesting paper on melanin
color formation[8] has shown that in all probability melanin
colors develop as the result of the action of an enzyme
upon a chromogen, and that this action is a complex one.
The chromogen is first converted into a new substance,
the same enzyme then converts this substance into a third,
and so on, producing a long series of substances. The
early numbers in this series give no color, but finally a
stage is reached where a number of steps in the series give
color. Riddle seems to think that all the melanin colors
found in organisms should be referred simply to the dif-

[8] *Biological Bulletin*, May 1909, pp. 316–351.

ferent stages of a single process of oxidation. This, how-
ever, can hardly be true. The fact that we get two or
three kinds of pigment deposited in the same region of the
organism, apparently at the same time, would indicate
that there is more than one oxidation process involved.
Furthermore, Riddle himself points out that, while in
some oxidation processes series of colors occur extending
from light yellow to black, with reds and browns as inter-
mediates, in others the final stages of the oxidation proc-
esses are red. Quite a number of different oxidation
processes are cited. Now the facts of color inheritance
indicate that there may be several oxidation processes,
and that in some of them a given color, for instance, red,
appears as soon as color appears at all.

Assuming that the production of enzyme and chromo-
gen is a general function of protoplasm, and assuming
further that the relative amount of enzyme and chromo-
gen present have a determining influence on the stage
which the oxidizing process reaches in the organism, the
phenomena of Mendelian color inheritance are easily ex-
plained without recourse to the idea of unit characters at
all, as I shall now attempt to show. It must be under-
stood that the figures in the following tables are merely
illustrative and are not meant at all to indicate actual
amounts.

TABLE I

RED AND WHITE PEAS

Organs.	RELATIVE CONTRIBUTIONS.		F_1	F_2		
	Pure Red.	Pure White.		BB	BB'	$B'B'$
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
Cy	25	25	25	25	25	25
AA	15	15	15	15	15	15
BB	30	10	20	30	20	10
CC	8	8	8	8	8	8
DD etc.	22	22	22	22	22	22
	100	80	90	100	90	80
	Red	White	Red	Red		White

Let us consider first the cross between red and white
sweet peas, in which generation F_1 of the hybrid is red
and generation F_2 gives us the ordinary Mendelian ratio

of three red to one white.   Table I shows an explanation
of the Mendelian results on the assumption that every
organ in the cell is concerned in color development.   It is
assumed in this instance, merely for purpose of illustra-
tion, that when the amount of enzyme present in the cell is
85 per cent. or more of the amount found in pure red races
the oxidation process reaches the stage necessary to pro-
duce red coloration.   The same end results would occur
if, because of some peculiarity of a *single pair* of chromo-
somes in the white race, as compared with the red, the
end result of the oxidation process in the white race gives
no color.

In the first column of this table Cy represents the cyto-
plasm, and, in fact, all of the organs in the cell except the
paired chromosomes. AA, BB, etc., represent pairs of
homologous chromosomes.   The second column gives as-
sumed relations between the amount, say, of the enzyme
produced by the different organs of the cell in the pure
red race.   It is assumed, for instance, that all the organs
of the cell except the chromosomes produce 25 per cent. of
this enzyme.   The first pair of chromosomes produce 15
per cent., the second pair 30 per cent., and so on.

Now, with the assumptions made, a white race would re-
sult if a single pair of chromosomes produce markedly
less of the enzyme than they produce in the red race.
Column 3 shows the hypothetical conditions in such a
white race.   In the table it is assumed that in the red race
the second pair of chromosomes produce 30 per cent. of
the total amount of enzyme present, while in the white
race, for some reason, this pair of chromosomes produces
only one third of the enzyme it does in the red.   Thus, in
the white race we have only 80 per cent. of the amount of
enzyme present in the red, and not enough to carry the
oxidation process to the point of giving red coloration.
The hybrid between these two races will have one chro-
mosome producing its 15 parts and another chromosome
producing only 5 parts, thus giving 20 parts where in the
red race we had 30.   In all, there is in the hybrid 90 per

cent. as much of the enzyme as in the pure red. With the assumptions made the hybrid would therefore be red.

It is well known that heterozygotes frequently present vegetative vigor much greater than that of the related homozygotes. This may be possibly due to the greater opportunity certain chromosomes have of making more growth before filling the cell with their products. If such is the case, then the enzyme produced in our hybrid might exceed the mean between that produced in the two races crossed. This would explain the preponderance of cases in which the heterozygote resembles that parent which represents the more advanced ontogenetic stage. But there are not a few cases in which the heterozygote resembles the other parent. This happens to be the case in two of the first cases of dominance made out by the writer; namely, beards in wheat and horns in cattle. Both of these characters are recessive; or, as the de Vriesians would say, in them, absence is dominant to presence. Under the present hypothesis, we do away entirely with the presence and absence hypothesis, as will be seen later.[9]

In generation F_2 (Table I) one fourth of the progeny would possess a pair of chromosomes each of which produces its 15 parts of enzyme. One half of the individuals would have one chromosome producing 15 parts and another producing 5, while the remaining fourth of the individuals would have a pair of chromosomes each of which produces only 5 parts. We thus have one fourth of the population producing the normal amount of enzyme, half of it producing 90 per cent. of this, and one fourth of it producing only 80 per cent. This would give us three red individuals to one white.

It must be remembered that I am merely attempting to show here that it is possible to make assumptions that will explain Mendelian phenomena without resort to the idea of unit characters.

In Table II we have a more complex case; namely, that of the cross between red and white *Antirrhinums* reported by de Vries. In this cross de Vries found what is ordi-

[9] See article by Shull in AMERICAN NATURALIST, July, 1909.

narily called two pairs of Mendelian characters. Under the assumptions I have made this simply means that in the white race there are two pairs of chromosomes which were deficient in the amount of enzyme produced as compared with the pure red race used by de Vries in this cross.

TABLE II

RED AND WHITE ANTIRRHINUMS

Organs.	Relative Contributions.		F_1	F_2								
	Pure Red.	Pure White.		$AACC$	$AACC'$	$AAC'C'$	$AA'CC$	$AA'CC'$	$AA'C'C'$	$A'A'CC$	$A'A'CC'$	$A'A'C'C'$
Cy	24	24	24	24	24	24	24	24	24	24	24	24
AA	30	14	22	30	30	30	22	22	22	14	14	14
BB	12	12	12	12	12	12	12	12	12	12	12	12
CC	26	22	24	26	24	22	26	24	22	26	24	22
DD etc.	8	8	8	8	8	8	8	8	8	8	8	8
	100	80	90	100	98	96	92	90	88	84	82	80
	Red	White	R	Red						Del.		Wh.

In the third column of Table II we have 14 parts of enzyme instead of 30 in the second column (chromosomes AA), and 22 parts instead of 26 in the second column (chromosomes CC). Since the hybrid gets one of each pair of chromosome from each of the parents it has 22 parts instead of 30, and 24 instead of 26. If, in this case, the amount of enzyme present in the cell is 85 per cent., or more of that present in the original red race with which de Vries worked, it is assumed that the oxidation process will reach the red stages. The hybrid in this case is red, though perhaps not so deep a shade of red as the pure red race.

In generation F_2 of this hybrid we have nine types. The first type is like the pure red race with which de Vries started. The third of these types is another pure race, but with a lessened amount of enzyme, and presumably less intense red color. The seventh type is also a pure race, but it is one which had only a little red at the margins of the petals and a type to which de Vries gave the name Delilah. The ninth type is also a pure race,

which has white flowers and is like the pure white parent used in the cross.

De Vries states that in the reds and the Delilahs found in F_2 there was a good deal of variation, which is what we might expect from the relations shown in Table II, but he was able to group them, as shown at the bottom of Table II, and get the usual Mendelian ratios.

I have assumed here that when the enzyme is present in proportions from 82 per cent. to 84 per cent. of that in the pure red race, we get the Delilah type. This merely means that in the Delilah types the amount of enzyme present is near the critical point for the production of red color. There seems to be no question that the environment in the organism itself is a very important determining factor in the development of any character. It is not therefore fanciful to assume that in view of the fact that we get color development only in the petals the tendency to color development might be greater in one part of the petal than in another. We thus see that our assumptions are in agreement with the facts of inheritance made out by de Vries.

Cryptomeric Characters

In one of Bateson's *Matthiola* crosses,[10] between a cream-colored and a white race, he found that the first cross was purple and that amongst its progeny it produced purples, reds, creams and whites. He explained these phenomena by assuming that red is due to two cryptomeric factors which are ineffective unless present in the same cell, while purple was due to a third factor which converted red into purple and which was found in the white variety. These phenomena may be brought in line with our hypothesis, as shown in Table III.

In this case we evidently have to deal with more than two chemical substances. For the production of the red character itself two of these substances are necessary. It is, of course, possible that in the simpler case considered earlier the same two substances, possibly others also,

[10] See Rep. III, Evolu. Com., Roy. Soc., 1906.

are responsible for red, but, there being a deficiency in only one of them, we get the phenomena considered in Table I.

TABLE III
CRYPTOMERIC CHARACTERS
Bateson's Matthiola Crosses

$R_1 =$ first factor for red; $R_2 =$ second factor for red.

$P =$ factor for purple. R_1 and R_2 produce red when present in greater proportion than 90 per cent. of normal amount in pure purples.

P converts red to purple when P is present in 90 per cent. of normal amount in pure purples.

Organs.	Cream var.			White var.			F_1		
	R_1	R_2	P	R_1	R_2	P	R_1	R_2	P
	%	%	%	%	%	%	%	%	%
Cy	18	20	24	18	20	24	18	20	24
AA	12	26	26	28	26	26	20	26	26
BB	14	16	12	14	16	12	14	16	12
CC	22	20	22	22	2	22	22	11	22
DD	18	18	0	18	18	16	18	18	8
	84	100	84	100	82	100	92	91	92

In the cross now under consideration we must assume that, taking the cream and the white races collectively, there are deficiencies in two substances necessary for the production of the red, as well as in the substance necessary for the production of the purple, or in one of the substances if more than one is necessary.

Let R_1 represent the first factor for red, R_2 the second factor for Red, and P the factor for purple. It is assumed that when either R_1 or R_2 is deficient to the amount of 10 per cent. of the amount of these substances found in pure purple races, the reactions will not reach the stage necessary for the production of red color, and that when there is a like deficiency in the substance necessary for transforming red into purple this transformation does not occur.

Column 2 of Table III shows the contribution of each of the cell organs to the substance R_1 in the cream variety; the next column gives similar data for substance R_2, and the next for the purple factor. The facts indicate that there is a deficiency in one pair of chromosomes (AA) for the substance R_1 in the cream variety; also for

the purple factor in another pair of chromosomes (DD). These deficiencies are italicized in the table. In the white variety there is assumed to be a deficiency for the substance R_2 in a third pair of chromosomes. These assumptions give the phenomena found by Bateson. A similar case is found in sweet peas.[11]

It is seen in Table III that the cream variety has less of R_1 than is necessary to produce red coloration. It also has less of the purple factor than is necessary for converting red into purple, while the white variety has less of the substance R_2 than is necessary for the production of red.

Generation F_1 will have enough of all these substances to produce red and to convert red into purple.

The second generation of this hybrid contains 27 types. I will not here go into detail concerning that generation, but will merely add that the assumptions made are consistent with the facts observed in the second generation.

TABLE IV
HETEROZYGOTE CHARACTERS

Spotted F_1 beans from non-spotted P_1's.

$S_1 = $ first factor of spotting; $S_2 = $ sec. factor of spotting. S_1 and S_2 assumed to become operative when present in greater proportion than 85 per cent. of normal in pure spotted beans.

Organs.	♂ Parent.		♀ Parent.		F_1	
	S_1	S_2	S_1	S_2	S_1	S_2
	%	%	%	%	%	%
Cy	40	30	40	30	40	30
AA	36	22	16	42	26	32
BB etc.	24	28	24	28	24	28
	100	80	80	100	90	90

Table III deals with cryptomeric characters which are seen to owe their development to the reaction between two, or possibly more, chemical substances, the production of each of which is a generalized function of the cell. It is, of course, possible that each of these substances is produced only by a single chromosome, which case would be merely a limiting case in which all the cell organs ex-

[11] Rep. III, Evolu. Com., Roy. Soc.

cept one produce none of a given substance in question.

Table IV deals with that class of characters which appear in heterozygotes, but not in pure races. Loche, Von Tschermak, Shull and Emerson have all studied such a character in beans. In certain crosses between beans not having spotted seeds the heterozygotes were spotted. Let us assume that the development of spotting on the seed coat is due to certain metabolic activities that involve at least two substances the production of which is either a generalized function of all cell organs or is a function of at least one pair of chromosomes. Let S_1 represent one of the substances necessary to these reactions, and S_2 another. Further, let us assume that in order to bring about the conditions necessary for the reaction both S_1 and S_2 must be present in a proportion 85 per cent. as great as in pure races of beans with spotted seed coats. In one of the races we assume a deficiency of substance S_2, and we assume that this deficiency is found in one pair of chromosomes only. In the other race there is a deficiency in substance S_1, and the same pair of chromosomes is responsible for this deficiency. Column 3 of Table IV shows 80 per cent. of the amount of S_2 found in ordinary spotted races of beans, while column 4 shows a similar deficiency in the substance S_1 in the other race.

Now generation F_1 of this cross receives one of the chromosomes in question from each of the parents, and in the case of each substance there is a deficiency of only 10 per cent. This gives us a spotted seed coat.

In the second generation, which is not shown in the table, one fourth of the progeny would be like the male parent and the other fourth like the female parent, neither of which has spotted seed coats, while half of the progeny would be like F_1 with respect to spotting of the seed coat.

While in this discussion it has been assumed that each of the substances with which we dealt was produced as the result of a general function of protoplasm, this is not necessarily the case. When we consider the history of the chromosomes it would appear very reasonable to

suppose that marked variation in the composition, and consequently in the functions, of the chromosomes may have occurred as a result of evolutionary changes. It may be that some of the substances with which we have dealt are produced only by particular chromosomes, but we can hardly decide this question with the evidence at hand. In any case, particular chromosomes must be responsible for the deficiencies of the substances in order to get Mendelian phenomena. As previously stated, my object is simply to show that it is possible to make assumptions that will give us Mendelian phenomena without unit characters. The assumptions made seem to be consistent with the facts of physiological chemistry.

Even if we assume that the various substances with which we have been dealing are each produced by a single pair of chromosomes rather than by all the organs of the cell we can not look upon the chromosomes as the hereditary units spoken of by the de Vriesians and Weismannians, for we here look upon each chromosome as playing possibly an important part in the development of every feature of the organism.

The fact that in some species the number of pairs of Mendelian characters found is greater than the number of chromosomes is not an argument against the validity of the assumptions I have made. In Table IV we have assumed that the same pair of chromosomes may be responsible in one race for the deficiency of a certain substance and in another race for the deficiency of another substance. It happens in this case that the two substances concerned are both necessary to a particular reaction. If each chromosome play its part in the development of all parts of the organism, we might, in different races of a species, have a good many Mendelian characters dependent upon the same set of chromosomes, and instances of this kind are not wanting. For instance, Bateson found a particular flower color and a particular shape of the standard in sweet peas to be alternative to each other in inheritance. In other words, in the terms of our theory we have here two pairs of Mendelian characters

based on the same pair of chromosomes. Several other
similar cases are known.   So that in order to prove that
anything smaller than a chromosome is responsible for a
Mendelian character difference it must be shown that we
can get into a single individual more independent Men-
delian character pairs than it has pairs of chromosomes.
Both Baur and Shull, in private correspondence with the
writer, have admitted the justice of this contention, and
have promised to put it to the test.

Under the present hypothesis what has heretofore been
called a pair of Mendelian unit characters must have a
new name.   For instance, in the red and white pea cross,
if our assumption regarding the cause of the Mendelian
phenomena is correct, we are not dealing with a pair of
characters at all in the de Vriesian sense.   Red is as-
sumed to be a generalized function of the cell, and white
likewise, but the difference between the red and the white
concerns a single cell organ, and it is this difference with
which we are dealing.   Dr. McDougal, in conversation
with the writer on this point a few days ago, suggested
that in discussing this hypothesis we use the term ''char-
acter differential'' instead of character pair, and the sug-
gestion seems to be a good one.   We do, however, need
a few terms, which I shall now proceed to introduce
Under our hypothesis each of the organs of the cell is
supposed to have various functions in development.   One
function may relate to the development of a particular
character, and another to a very different character.
Furthermore, several or all the organs in the cell may
each have a function relating to the same character.

But not only are the organs of the cell supposed to play
their part in development, but various organs, tissues and
substances produced in the organism during development
may also have functions which play a part in the develop-
ment of various portions of the organism.   For instance,
hairs normally develop only in the skin.   Hence the skin
itself influences the development of hair.   It is supposed
that certain substances, called hormones, may materially
affect the development of parts of the organism widely

separated from the part of the organism in which these substances are produced. Thus the greater development of horns in the males of certain species is supposed to be due to hormones produced in the testes.

Any organ, tissue, substance or cell organ which thus has the power of influencing the course of development, I propose to call a "teleone." This word is from the Greek *teleo,* which means *make,* or *accomplish.* Teleones occurring in the egg, and presumably derived directly from the previous generation, may be called primary teleones. Those that arise during the course of development may be called secondary teleones. The manner in which primary teleones function in heredity has already been indicated. In a simple Mendelian character difference we are thus dealing, not with two unit characters, nor with the presence and absence of a single unit character, but with a difference between two teleones.

Under this hypothesis, transmission becomes, not the transmission of characters as such, but the transmission of cell organs having functions which determine character, or which influence development. This hypothesis may properly be called the teleone hypothesis.

A word about species crosses. We may imagine that, in species not closely related, the corresponding teleonic functions all differ more or less; hence we should not expect many simple Mendelian phenomena in such crosses. Again, in wide crosses, it will probably happen frequently that the chromosomes brought together will be so dissimilar that they do not act together in the usual manner, especially in the reduction division. We should expect Mendelian phenomena only in cases where homologous chromosomes go through synapsis and reduction in a formal manner.

Finally, when character differentials relate to anything other than chromosomes, Mendelian splitting should not occur. I would therefore suggest that some of the character differentials studied by Castle in rabbits are due to cytoplasmic differences, or at least are not due to the chromosomes.

THE EVOLUTION OF NEW FORMS IN VIOLA THROUGH HYBRIDISM[1]

PROFESSOR EZRA BRAINERD

MIDDLEBURY, VERMONT

DURING the past eight years I have given much time to the study of our North American violets, not only as represented in large herbaria, but especially as seen in living specimens, both in their natural surroundings and under culture. My garden now contains over 3,500 violet plants of about 650 different numbers or sorts, some 200 of which are from the wild, and 450 raised from seed.

The genus has for over a century been known as difficult and perplexing because of its polymorphism. It has been my good fortune to discover that this is largely due to the frequent occurrence of hybrids between species of the same group. I make out to date some 66 different hybrids that have arisen spontaneously. From about 50 of these I have raised offspring that segregate, often in a surprising manner, reverting variously to the characters of the putative parents of the hybrid. In many cases I have raised from the hybrid two, or even three, generations of offspring.

But not all the anomalous violets that I have grown and propagated can be called hybrids. Hybrids in *Viola* may be known by two marks: first, they are either completely sterile or markedly infertile; secondly, their seedlings are strikingly unlike each other, and often unlike the mother plant. The other class of anomalous violets are normally fertile, and come true to seed; they are often of sporadic occurrence, or if appearing in two or three stations, the stations may be hundreds of miles apart; furthermore, they usually present a mixture of the characters to be

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found in some two of the species with which they grow.
These odd forms, of which I have noted nearly a hundred,
are, in my opinion, largely the *result* of hybridism in the
remote or recent past.   The detailed evidence of this can
not be presented in a twenty-minute paper; it demands a
printed essay with abundant illustration.   I shall here
attempt only a brief summary of methods and results.

I would first call attention to the transitory existence of
a hybrid, especially when self-fertilized, as is usually the
case in *Viola*.   This follows from the laws of Mendel as a
mathematical corollary, though I am not aware of any
paper in which these deductions have been clearly set
forth.   Mendel, indeed, showed that in the case of the
monohybrid (where the parents differ in only one char-
acter) the offspring in the first generation are one half
stable, in the second three fourths stable, in the third
seven eighths, and so on; until in the tenth generation
there is on the average only one hybrid in 1,024 plants.
But it can be proved that where the parents differ in
two characters there will be on the average in the tenth
generation only two hybrids in 1,024 plants; where the
parents differ in three characters, there will be less than
three hybrids in 1,000 plants: where they differ in four
characters, less than four hybrids in 1,000; and so on.   In
the ordinary hybrid over 50 per cent of the offspring in
the fourth generation will be stable; in the sixth genera-
tion over 85 per cent will be stable; in the eighth genera-
tion over 95 per cent; in the tenth generation over 99
per cent.   The life of the self-fertilized hybrid is there-
fore always precarious and relatively brief.   The organ-
ism is in unstable equilibrium, and is rapidly shifting into
conditions of stability.

But the stable forms that emerge are not, as a rule, the
forms found in the parents of the original hybrid.   They
are exclusively such only in the case of the monohybrid;
in hybrids of a higher grade the stable forms consist of all
possible recombinations of the opposed characters of the
parent species.   Two species that differ in six characters

are capable when crossed of giving rise to 64 distinct and stable forms; if they differ in eight characters, of giving rise to 256 stable forms; if in ten characters, of giving rise to over 1,000.

One or two particular cases must suffice to illustrate how new and stable forms are artificially produced by the propagation of hybrid offspring. In September, 1905, with Mr. Witmer Stone, of Philadelphia, I visited Ivy Hill Cemetery, an interesting violet station, from which the previous May he had sent me several anomalous forms of *Viola*. Two of these proved to be hybrids of a species since named *V. Stoneana;* one with *V. papilionacea,* and the other with *V. triloba*. *V. Stoneana* has palmately dissected leaves and light-yellow seeds; *V. papilionacea* has undissected leaves, and dark-brown seeds. Among the progeny of their hybrid has appeared a form with the undissected leaves of *V. papilionacea* and the light-yellow seeds of *V. Stoneana*. This form comes true to seed (as was to be expected, since both characters presented are recessive), and shows no longer any marks of hybridity or infertility. Thus has appeared in the garden a stable variety of *V. papilionacea* with light-yellow seeds.

In the second hybrid, *V. Stoneana* × *triloba,* both parents have dissected leaves, though of unlike pattern; but *V. triloba* differs from *V. Stoneana* in being markedly pubescent. The first sowing of the hybrid seed gave me only four plants, one quite glabrous, three quite pubescent. Seeds of these were sown the following year, and from one of the three pubescent plants were obtained nine offspring, all pubescent with the leaf-form of *V. Stoneana*. So here we seem to have a pure dominant—a stable ex-hybrid—a new and pubescent variety of *V. Stoneana*. Just such a plant was once sent me by Mr. House, collected in the vicinity of Washington.

Leaving now the many cases of dehybridization in *Viola,* that have arisen in a few years of garden culture, let us glance at the evidence that this same process is going on in a state of nature, and has probably been going on for centuries.

Viola cucullata is a well-marked species of wide distribution, but it exhibits many anomalous forms; or as some would say, it is "an aggregate species." The capsules are a clear green in the numerous specimens that I have seen, with one exception. A plant, sent me by Miss Ryon from East Lyme, Conn., has dark-purple capsules; it is quite fertile, breeds true to seed, and in all respects but capsule color is normal *V. cucullata*. How shall we account for this aberrant form? Fortunately, with this plant was sent also from the same colony a hybrid of *V. cucullata* × *sororia*. The latter species at this station, as often elsewhere has very dark-purple capsules; may we not reasonably believe that the purple-fruited *V. cucullata* is a Mendelian product of the hybrid with which it was growing?

Viola cucullata is normally a very glabrous plant. But I have received forms of *V. cucullata* that were decidedly pubescent, from three widely separated stations: Mt. Mitchell, N. C., Milwaukee, Wis., and Salamanca, western N. Y. The plant from Wisconsin has a roundish leaf that resembles that of *V. sororia,* a pubescent species found at the same station. It is quite likely, therefore, that both the leaf-outline and the pubescent peduncles of the aberrant plant have come about through a former cross between the two species.

In October, 1906, I received indirectly from Miss Mulford, of Hempstead, Long Island, a plant of *V. affinis* that had black seeds. The species, which is as widespread as *V. cucullata,* has normally pale-yellow seeds. I noticed that the black seeds of Miss Mulford's plant were also somewhat larger than the ordinary yellow seeds of *V. affinis*. A careful weighing of 200 well-dried seeds of each lot shows the black seeds to be 49 per cent. heavier than the yellow seeds. I surmise, therefore, that the anomalous form is a by-product of *V. affinis* × *papilionacea,* a hybrid from which I have obtained forms in the garden similar to Miss Mulford's. I should add that though the black seed-color is dominant over the pale

yellow, two generations of offspring from the Mulford plant show the black color to be stable.

Just the opposite effect has been brought to pass in certain plants of *V. nephrophylla,* a northern species ranging from eastern Quebec to the Rocky Mountains, and having black seeds in all the many specimens seen, except the one here discussed. This plant with buff seeds appeared in a parcel of *V. nephrophylla* sent from Lake Nemahbin, Wis., in 1907, by Dr. Ogden, of Milwaukee. The plant was in all other characters good *V. nephrophylla;* the capsules were crowded with seeds which for two generations have in turn produced plants with like buff seeds. Now from the same region Dr. Ogden sent me a few days later the hybrid *V. affinis × nephrophylla,* seeds from which the following year gave plants with buff as well as with black seeds. It is therefore probable that the fertile and stable buff-seeded *V. nephrophylla* from Lake Nemahbin is the descendant of a hybrid of this species with buff-seeded *V. affinis.*

Many similar cases have come under observation. In a limited region in Salisbury, Vt., of less than a square mile, there occurs not infrequently a very pubescent form of *V. latiuscula,* a species which in all other stations I have found to be quite glabrous. On the other hand, from three stations I have obtained perfectly glabrous plants of *V. palmata,* a species normally pubescent. The plants from two of these three stations were somewhat infertile, thus betraying their hybrid origin.

The effect of hybridism is plainly to be seen in the numerous intergradient forms that occur between closely allied species of *Viola.* Take, for example, *V. fimbriatula* and *V. sagittata,* merged into one species by Dr. Gray, probably because of this intergradience. The extreme forms differ chiefly in three particulars: the leaf-blade of *V. sagittata* is narrowly lanceolate, glabrous and coarsely toothed at the base; that of *V. fimbriatula* is oblong-lanceolate, pubescent and not coarsely toothed at the base. But not infrequently we find colonies of *Viola fimbriatula*

with leaves that *are* coarsely toothed at the base, and col-
onies of *V. sagittata* with decidedly pubescent leaves; in-
deed, this is the prevalent form in the middle west.
Where the two species grow together, these and various
other interchanges of characters are frequent, in accord-
ance with Mendelian principles of segregation. A like
interchange of characters is noticeable in the stemless
white violets, *V. blanda, V. renifolia* and *V. incognita;*
and also in the stemmed yellow violets, *V. pubescens* and
V. scabriuscula.

We often find in species of wide distribution, as for
example *V. affinis* or *V. papilionacea,* numerous forms
distinct in one or more characters. Those who are so in-
clined can break up any one of these species into a dozen
or more ''elementary species,'' as some European botan-
ists have done with *V. tricolor.* But there are also cer-
tain species of *Viola* that are not polymorphic though of
fairly wide distribution; for example, *V. rotundifolia, V.
Selkirkii, V. hastata;* and it is worthy of note as bearing
upon the thesis of the present paper, that these species
have never been found to hybridize.

It frequently happens that a subhybrid form in *Viola*
is so unlike either parent of the first-cross as to appear to
be specifically distinct. Many such violet hybrids have in
recent years been named and published as species: *V.
Mulfordæ* Pollard, *V. notabilis* Bicknell and *V. aber-
rans* Greene are examples. It is surely hazardous in our
present knowledge of the genus to put forth as a species
a newly discovered form of *Viola,* without studying it
through at least one season of growth and through one
generation of offspring. It may, indeed, transpire that
the new form, though of hybrid origin, is distinct and
stable; and if fairly wide-spread, it may be entitled to
specific or varietal rank. The bar sinister in the escutch-
eon of its bastard ancestry may have been quite oblit-
erated. We may be here witnessing the birth of a new
species through hybridism. Allow me in closing to pres-
ent an instance that makes a close approach to these con-
ditions.

In May, 1906, Mr. Stone sent me from Tinicum, Pa., a living violet plant that was quite fertile and appeared a good species. I could not make it out a hybrid, though perhaps predisposed at that time to place an anomalous form in this category. For further light I visited the station with Mr. Stone the following September; but the most careful search failed to reveal another specimen. It soon afterward occurred to me that it might be an offspring of *V. affinis* × *sagittata,* a hybrid which I had found at the same place the year previous, and had transferred to the garden. The two plants, mother and supposed daughter, appeared much unlike, the former being quite infertile, and in most respects an excellent intermediate between the putative parents that grew near by. But careful examination showed that, though no one character of the supposed daughter was intermediate as in the mother, yet *all* were to be found in one or the other of the supposed grandparents. The leaves had the breadth and the rounded basal lobes of *V. affinis,* but the length and the attenuate apex of *V. sagittata;* the capsules were pubescent as in *V. affinis,* but green and large as in *V. sagittata;* furthermore, the peduncles were strictly erect as in *V. sagittata,* not ascending as in *V. affinis;* and also the seeds were brown as in *V. sagittata,* not buff as in *V. affinis.*

The next move was to raise offspring of the plant, to discover if some one of these characters was not impure —in other words, dominant and holding latent the opposed character. The 23 plants subsequently raised showed all the characters of the plant under investigation to be pure excepting two, the pubescence of the capsules and the dark-brown color of the seeds; for glabrous capsules and buff seeds appeared in some of the offspring. The ratio of the four Mendelian forms in the 23 plants was $12:4:4:3$, or $9:3:3:2\frac{1}{4}$, an unexpectedly close approximation to the theoretical ratio $9:3:3:1$.

From eleven of these plants another generation of 204 plants was raised the past season. Among these, in addi-

tion to the five possible hybrid forms, were obtained also the four possible stable forms. So that I now have fertile plants, free of all hybridity, of four sorts, viz., 18 with pubescent capsules and dark seeds, 9 with pubescent capsules and buff seeds, 18 with glabrous capsules and dark seeds, 44 with glabrous capsules and buff seeds.

Surely, what I have done in the garden, nature might do in the wild, thus evolving a distinct species with three varieties.

In justice to my subject let me say that I am far from maintaining that hybridism is furnishing in the genus *Viola* all the new forms for natural selection to work upon. Hybridism adds no new character to a group of species; it simply recombines in multifarious ways characters already existing. However numerous the patterns that appear in the revolving kaleidoscope, their number is limited; and if we looked long enough we should find them substantially recurring from time to time. To get a strictly new pattern, we should need to insert in the apparatus a new fragment of colored glass. In the evolution of living organisms the new piece of colored glass is what the biologists are considering under the name of mutation.

TERTIARY ARCHHELENIS

DR. A. E. ORTMANN

CARNEGIE MUSEUM, PITTSBURGH, PA.

THE *Archhelenis-theory* of von Ihering has now received so much support from various sides that we may regard it as firmly established with regard to its general correctness. Stated in broad terms, this theory assumes a former land connection between Africa and South America, which is rather old. This connection is the last remnant of a large southern continental mass (South Atlantis, Gondwana-land), which existed since the beginning of the organic history of the earth (Cambrium), which was broken to pieces at different times, and the remnants of which are now found in Australia, India, Africa and Brazil. The separation of Brazil from Africa was the last step in the dismemberment of this old continent, an event which is placed by most writers toward the end of the Mesozoic era, although some have admitted the possible continuation of Archhelenis into the beginning of the Tertiary.

Recently, von Ihering has tried to fix the time of the disappearance of the connection between Africa and Brazil more exactly, and arrived at the conclusion that Archhelenis *persisted* at least through the *Eocene*. He discusses the question chiefly in connection with his studies on the marine fauna of the Patagonian beds, which he regards as Eocene.[1] Comparing this fauna with the contemporaneous Tertiary faunas of the rest of the world, he discovers certain facts, which, according to him, can not be explained except by the assumption that Archhelenis was still in existence at the beginning of the Tertiary.

[1] Ihering, H. von, "Les Mollusques fossiles du Tertiaire et du Crétacé supérieur de l'Argentine," *Anal. Mus. Buenos Aires,* 14, 1907.

I fully accept the facts of the faunistic relations of the
Patagonian beds, as laid down by von Ihering. Yet I do
not believe that they demonstrate the necessity of assum-
ing the existence of Archhelenis at that time, but, on the
contrary, I believe *that they point just to the opposite,*
namely, that at the time when the Patagonian beds were
deposited (in the early Tertiary—it does not matter, for
the present purpose, whether we regard the beds as
Eocene or younger) the connection between Brazil and
Africa must have disappeared, and that there must have
been a deep ocean in its place.

Of the relations of the Patagonian fauna to other
faunas, the following are mentioned by von Ihering as
most important (p. 76 ff.).

While the Patagonian fauna in general is very peculiar,
and consists preeminently of southern (antarctic) ele-
ments, yet there are certain affinities to Tertiary faunas
of the northern hemisphere. But there are hardly any
relations to North America, and the few affinities with
northern faunas are rather with the *Indo-European
fauna.* This, of course, means that the Indo-European
forms, which may be regarded as constituting resem-
blances with the Patagonian fauna, are *not* found in
North American Tertiaries. Von Ihering believes that
these peculiar conditions are to be accounted for by the
existence of a land barrier between the North and the
South Atlantic, which prevented a migration of North
American marine forms to Patagonia, while there was a
possibility for Patagonia to receive Indo-European types
from the Indian ocean along the eastern coast of Africa
and the southern coast of the Atlantic land-connection
(Archhelenis).

While I do not doubt the correctness of the view that
Patagonia did not receive the Indo-European elements
of its fauna by the direct way, from the Mediterranean
across the Atlantic, I think, the fact of the *absence* of
these forms from North America is not correctly under-
stood and interpreted by von Ihering. If Archhelenis

existed at that time, there must have been *a coast line*
not only in the south, but also in the north of this land,
*running across the present Atlantic from North Africa
to the West Indies.* Since the forms under discussion
are most emphatically marine littoral-shells, such a coast
line would have favored their migration from the Euro-
pean waters to those of the West Indies and North
America. Thus these forms, which are found both in the
Patagonian and in the Indo-European Tertiaries, should
have been able, by all means, to reach also North Amer-
ica. The fact, however, that they are absent in the latter
parts indicates decidedly, that there was no possibility
for them to go across the Atlantic from Europe to Amer-
ica, and thus there can not have been a coast line or a
land connection between Africa and South America, but
there must have existed a deep ocean (the Atlantic),
which prevented their migration from Europe to North
America as well as from Europe by the direct way to
Patagonia.

One fact, however, remains now unexplained, namely,
the absence of North American types in Patagonia. If
the Atlantic Ocean extended uninterruptedly from
north to south, as it does now, there must have been, dis-
regarding small interruptions at Panama and in the
region of the Amazonas, a rather continuous shore line,
along which the northern forms could have migrated to
Patagonia. I think such a north-south migration actu-
ally took place, but it did not reach the southern extrem-
ity of South America on account of climatic differentia-
tions along this coast line. Von Ihering points out (p.
492) that the Patagonian fauna is characterized by the
absence of certain types of shells, which are preeminently
tropical. This very strongly suggests that the Patago-
nian Tertiary seas were not of a tropical, but of a sub-
tropical or even temperate, character. If this is true, it
is apt to furnish an explanation for the absence of North
American forms in Patagonia. The North American
fauna of the Tertiary is found from Florida to New

Jersey, and some of the richest deposits are in Florida and Alabama, parts which surely had a tropical climate in the beginning of the Tertiary. If Patagonia was ex-tratropical, we can not expect that this fauna should have reached it, for its southward migration would have been stopped by the southern boundary of the tropical belt.

On the other hand, von Ihering points out that, while there was no immigration of tropical West Indian and North American types during the Patagonian time, such an immigration took place later, when the Entrerios beds were deposited (which he believes to be Miocene), for we find such forms in these beds. He thinks that it is thus demonstrated that the destruction of Archhelenis falls in the time between the deposition of the Patagonian and Entrerios beds. I can not admit this, for the Patagonian beds are found far to the south (between 45 and 50° S. lat.), while the Entrerios beds are in 30–35° S. lat. It is true, there are localities for Entrerios beds farther to the south (as far as about 43° S. lat.), but of the character-istic tropical types, which are named by von Ihering (on p. 361) not a single one is found at these southern locali-ties (see table on pp. 357 and 358). Thus it is very prob-able that, while at the time and the locality of the depo-sition of the Patagonian beds an extratropical climate prevailed, a tropical climate may have existed at the same time farther north (north of say about 40° S. lat.). However, we do not know the corresponding deposits of these parts, and we only know that there are tropical im-migrants in later deposits in about 30–35° S. lat., but this does not prove that there were no such in the north-ern parts of Argentina at the time of the deposition of the Patagonian beds. In fact, the presence of certain tropical types in the Navidad beds of Chile (p. 514), which very much resemble the Patagonian beds in gen-eral character, but are situated a good deal farther north, suggests strongly, that the Navidad beds are the tropical "facies" of the Patagonian beds. I do not think

that a separation of the Patagonian and Chilean sea by land is to be assumed for the explanation of the absence of these tropical types in the Patagonian beds, as von Ihering is inclined to do (p. 495). Of course, the Patagonian beds were deposited on the east side, those of Navidad on the west side, of the old peninsula extending northward, and now represented by the Chilean Coast Cordilleras, but this peninsula had an end somewhere to the north, and around this point a communication of the two seas was possible, till the elevation of the Cordilleras de los Andes took place, and connected the old Chilean land with the land lying to the east of it.

Further, if there was no connection of Africa and Brazil any more in Tertiary times, the migration of the Indo-European forms to Patagonia by the route indicated above (East Africa, and south coast of Archhelenis) was impossible. Yet there is another way open. As von Ihering points out (p. 81), this Indo-European fauna reached eastward to Australia and the Pacific Islands, and thus it very likely does not originally belong to the fauna of the old Tethys (Mediterranean, North Atlantic, West Indian seas), but consists of old Pacific elements which extended, in the Tertiary, eastwards into the Mediterranean part of the Tethys (Europe). The very absence of these types in the West Indies and in North America supports this view. And further, since the Antarctic fauna, to which the Patagonian fauna shows the closest affinities, is nothing but an offshoot of the old Pacific fauna, the relations of the Patagonian to the Indo-European forms find thus their explanation, and the way, by which these faunas are connected, apparently goes over Australia and Antarctica.

Finally, for the non-existence of Archhelenis in the Eocene very recently a new line of evidence has been introduced. Stromer[2] points out that recently quite a number of marine Eocene deposits have been discovered

[2] Stromer, E., ''Ueber Alttertiaer in Westafrika und die Suedatlantis,'' *Jahrb. kgl. Preuss. Geol. Landesanst.*, 30, 1909, p. 511 ff.

in West Africa, namely, in the region south of Sene-
gambia; on the middle Niger River; in the southern
central Sahara and in northern Nigeria; in Togo and
Cameron (Gulf of Guinea); and even as far south as the
Gabun, Angola and Mossamedes.   Although these de-
posits are rather scattered, their Mediterranean character
has been recognized, so that it appears as very probable
that they belong to a continuous sea, which extended
south from western Europe along the west African coast.
That is was actually continuous is demonstrated, accord-
ing to Stromer, by the distribution of the Nummulites
in these beds, which are found only in the north, and
indicate a cold northward current along the west African
coast: such a current could develop only under a similar
distribution of land as at present, namely, if the
west African coast extended uninterruptedly from south
to north, as it now does.   This, of course, would show
that the Atlantic at that time existed approximately in
its present form, its northern (Tethys) and southern
(Nereis) parts being connected, and that the separating
land bridge, Archhelenis, had disappeared.

All the above considerations lead us only to one con-
clusion: that *in the beginning of the Tertiary Archhelenis
had ceased to exist, and that there was no connection any
more between South America and Africa.*   Indeed, the
facts introduced by von Ihering in support of his assump-
tion of the existence of this land-bridge in the Eocene,
prove to be, under renewed critical investigation, *the
strongest evidence for the contrary,* and it has been shown
above that also some other facts, which apparently con-
tribute to the support of von Ihering's view, may be
easily understood under the assumption that *Archhelenis
had been destroyed at the beginning of the Tertiary
time.*

SHORTER ARTICLES AND DISCUSSION

THE PROBABLE ORIGIN OF THE CRINOIDAL
NERVOUS SYSTEM

ALTHOUGH at first sight the nervous system of a crinoid appears to be so radically different from that of an invertebrate of the more usual bilateral type that no satisfactory comparison is possible between them, I believe that there is no difficulty at all in deriving it from the latter.

The nervous system of a crustacean, worm or insect consists typically of a supraœsophageal ganglion united by a pair of circumœsophageal ganglionic connectives to a more or less marked subœsophageal ganglion, from which there runs back along the ventral side of the animal a long nerve cord, or pair of nerve cords, marked at intervals with ganglia. The anterior end of the digestive tube passes between the two chief ganglionic masses, as the names of all these structures indicate.

The ancestral crinoid was bilateral, and therefore possessed a nervous system constructed according to this plan. With the progressive decrease in directive locomotion the ventral nerve cord was correspondingly shortened, concurrently with the assumption by the animal of a more compact form, just as the nerve cord has been shortened in *Cancer* as compared with *Palinurus,* in *Dynamine* as compared with *Apseudes,* in *Cimex* as compared with *Diapheromera,* or, better, in the crustaceans as a class as compared with the annelids as a class. In the crinoids the shortening progressed still further; locomotion, other than casual or accidental, ceased; the anterior end of the intestinal canal became deflected upward and pressed upon the anterior part of the supraœsophageal ganglion which gave way before it and became deeply crescentic; at the same time the ventral nervous cord was retracted into a short protuberance from the subœsophageal ganglion. Finally the horns of the crescent formed from the supraœsophageal ganglion met in front of the throat so that what was originally a ganglion mass became a nerve ring, the two connectives became broken up into numerous connecting fibers, and the whole ventral nerve cord with its

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ganglia became retracted into the subœsophageal ganglion, now become the dorsal nerve mass.

Thus we may very easily derive the radiating nervous system of the crinoid from the bilateral nervous system of the arthropod, the circumoral nerve ring of the crinoid being derived from the supraœsophageal ganglion of the arthropod, and the dorsal nervous system from the subœsophageal ganglion. In this connection it is significant that the circumoral nerve ring innervates the same structures and possesses the same functions as the supraœsophageal ganglion, while the dorsal nervous system is identical with the subœsophageal ganglion, plus the ventral nerve cord, in the nature of its duties.

The assumption of the pentaradiate form by the crinoids has produced a complex condition of orientation; for the so-called "ventral" surface of the crinoid, in terms of arthropod or annelidan orientation, is equal to the anterior end, plus the posterior end, and plus such part of the dorsal surface as is not shoved to one side by the approximation of the two extremities of the intestinal canal; while the "dorsal" surface of the crinoid is the equivalent of the entire *ventral* surface of the arthropod, plus more or less, possibly nearly all, of the dorsal surface.

<div align="right">AUSTIN H. CLARK.</div>

NOTES AND LITERATURE

RECENT LITERATURE TOUCHING THE QUESTION OF SEX-DETERMINATION

In 1889 Geddes and Thomson in their book on the "Evolution of Sex" stated that "Nutrition is one of the most important factors in determining sex" (p. 47), and developed the theory that "Anabolic conditions favor the preponderance of females, katabolic conditions tend to produce males" (p. 47). In the revised edition of 1901 practically the same idea is stated thus: "The female is the outcome and expression of relatively preponderant anabolism, and the male of relatively preponderant katabolism" (p. 140). The following year (1902) Beard[1] expressed the conclusion, based upon considerable evidence, that: "Any interference with, or alteration of, the determination of sex is absolutely beyond human power. To hope ever to influence or modify its manifestations would be not less futile and vain than to imagine it possible for man to breathe the breath of life into inanimate matter" (p. 763).

The two fundamental ideas here expressed—namely, that the nature of the environment (chiefly the amount of nutrition) may determine the sex of the developing germ, *i. e.*, that sex is quantitatively determined; and that sex is predetermined in the germ, *i. e.*, qualitatively (independently of external conditions if only they be favorable to development) have until recently sharply divided investigators on the problems of sex. Both positions seemed about equally well supported by numerous facts both experimental and cytological for animals, and experimental for plants. In only a few instances has opinion been divided over the same form; in the majority of cases the results appeared convincingly in favor of one or the other view.

The more recent tendency seems to be to interpret sex-determination (at least proximately) as the result of a quantitative relation between karyoplasm and cytoplasm in the fertilized ovum, or more strictly, between chromatin and cytoplasm. This position rests upon the observation chiefly that in those insects where heterochromosomes have been described the eggs which develop into females contain the greater amount of chromatin material (exceptions—*Metapodius*, Wilson; and possibly *Acholla*,

[1] Beard, John, "The Determination of Sex in Animal Development," Jena, 1902.

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Payne), and has been suggested as probable more particularly by
Morgan and by Wilson. The former,[2] however, regards the
quantitative interpretation of sex-determination as only the
"first rough approximation" (p. 348) to the solution; and the
latter[3] inclines to the belief that "if the idiochromosomes be sex-
determinants their difference is probably a qualitative one" (p.
189), though this may possibly be a difference merely of degree
of special activity.

Boveri's[4] generalization that the cytoplasm and nucleoplasm
of cells bear to each other a constant ratio, and that "a ferti-
lized egg that contains more chromatin is a potentially larger
cell than one with less chromatin" (pp. 9–10) may help to recon-
cile the conflicting theories. If the amount of chromatin may
be rightly taken as an index of the state of nutrition or poten-
tial anabolic capacity, the apparently contradictory facts that
nutrition (environment) in one case and internal factors (per-
haps simply more or possibly more active chromatin) in the
other case determine sex, can be harmonized. If chromatin and
chromatic substances (nucleo-proteids) may be regarded as food
material or active agents in constructive metabolism, the better
nourished gametes (or such as contain more chromatin) appear
destined to produce the female sex, the less well nourished the
male sex.

Several recent investigations again affirm the opposing views,
well supported with experimental or cytological facts, though a
reconciliation is suggested from both sides on the basis of a
quantitative relationship signifying in one direction high metab-
olism (anabolism) and in the other low metabolism ("relatively
preponderant katabolism").

The most important recent paper concerning the question of
the determination of sex is that of Russo.[5] This author takes
issue with the prevailing hypothesis which views the chromo-
somes as the vehicles of the determinants of hereditary charac-
ters, and objects more especially to a Mendelian interpretation of

[2] Morgan, T. H., "A Biological and Cytological Study of Sex Deter-
mination in Phylloxerans and Aphids," *Journ. Exp. Zoöl.*, Vol. 7, no.
2, 1909.

[3] Wilson, E. B., "Studies on Chromosomes, V." *Journ. Exp. Zoöl.*,
Vol. 6, no. 2, 1909.

[4] Boveri, Th., "Ueber Beziehungen des Chromatins zur Geschlechts-
Bestimmung," *Sitz. Phys. med. Gesell. Wurtzburg.*, Jahrgang 1908–1909.

[5] Russo, A., "Studien ueber die Bestimmung des weiblichen Gesch-
lechtes," Jena, 1909, pp. 1–105.

sex-phenomena. The fact that in the gametes, particularly the eggs, besides certain phosphorus-containing proteins, lecithin is abundantly present, suggested a series of experiments to determine whether the lecithin content of eggs could be artificially increased and whether such accession could produce a significant physiologic modification in the germ-cells.

Russo finds that normally in rabbits and various other mammals the lecithin content of eggs of the same ovary varies greatly; some containing much, others little. This variable cell condition indicates a shifting chemical state, expresed morphologically in the form of "chromidial-bodies" (mitochondria, chondriomites, pseudochromosomes, chromidial net, etc.). These structures Russo has succeeded in producing by artificial means (*i. e.*, injection of lecithin), and he regards them as having "no small influence on developmental phenomena." He does not deny that the nuclear chromatin plays an important rôle in development, but he refuses to regard it as alone the material basis of heredity. The nuclei may assist in the process of heredity, but the results of his investigations on rabbits indicate that sex and other "unit characters" (*e. g.*, pigmentation) are a function of the degree of cell metabolism.

Russo believes that "contrary to the chromosome theory, the characters of Mendelian hybrids in the first or dominant generation, especially as concerns the pigmentation and color of the hybrid, do not bear any absolute relation to the chromosomes, but that they depend in greatest part upon a specific metabolism or chemical condition residing in the egg cytoplasm; that, further, the sex of the offspring depends upon a special metabolism (Stoffwechsel) of the germ-cells, and that by artificial modification of the chemical or metabolic state (Metabolismus) of these elements the Mendelian law (*i. e.*, of dominance) can be modified in that one may fix this or that most recent variety, as it is also possible at will to determine the sex" (p. 4).

Lecithin was administered subcutaneously, intraperitoneally and per os. The ovaries of lecithin-fed rabbits attained a size three times as great as that of ordinary individuals and contained much larger Graafian follicles. Under such treatment the germ cells became markedly anabolic. Russo notes that in normal ovaries some ova contain much deutoplasmic material in the zona pellucida and the vitellus, and others little or none. The artificially highly nourished eggs produce females; and the lecithin-fed individuals give rise preponderatingly or even ex-

clusively to female offspring. There are thus in rabbits two kinds of eggs corresponding, respectively, to each sex: (1) well nourished, highly anabolic, or female; (2) poorly nourished, slightly anabolic (or katabolic) or male.

The sperm, containing chemical substances similar to the eggs, are regarded as merely giving aid in the development of a process already begun in the egg leading towards the determination of a particular sex. That the sperm has a complementary and not an antagonistic rôle in sex-production seems established by the fact that the percentage of female offspring is higher when both male and female have been subjected to the lecithin treatment before union.

For the experiments Russo employed selected and ordinary varieties of rabbits. His chief aim was to "fix" a particular "unit character" of the female in the offspring (mostly female) of the first hybrid generation. The character selected was the color of the hair. Females of recent races characterized for hair color, i. e., white (albino, Himalaya, Angora, etc.), were crossed with males of various phylogenetically older races (e. g., "Grigia"—gray, and "Nero"—black). The best results were obtained from crosses between Himalaya females and "Nero" males. On crossing females of either albino or Himalaya races with males of "Grigia" and "Nero" stocks the offspring of the first generation always had the color of the male, i. e., gray or black, respectively, showing that these crosses ordinarily conform to the Mendelian law of dominance. Moreover, Russo notes that in nature the number of male offspring always exceeds that of the female, the percentage of the former being variously given as from 52 to 58 per cent.

When the same females were subjected to the lecithin treatment before conception, the offspring of crosses similar to the above were in the first generation preponderatingly of the type of the newer or female race. There frequently appeared atavistic exceptions, interpreted as due to a late ripening of the eggs concerned which consequently remained unaffected by the lecithin.

The most clear-cut result was obtained from the following experiment: A preliminary experiment, several times repeated, having shown that the ordinary cross conformed to the law of dominance, a young well-nourished "Polacca" (white) lecithin-treated female was crossed with a "Nero" male (black). The resulting progeny included 6 females (5 white) and 2 males (1

white), showing clearly that the female subjected to lecithin treatment yields a preponderance of females (with the maternal somatic character of hair color).

Occasionally the cross between a lecithin-fed Himalaya female and a normal "Nero" male resulted in several modified Himalaya offspring (*e. g.*, black legs or dusky coat, etc.) among the preponderating Himalaya hybrids. This condition is readily explained by assuming that in such crosses "the modification of the vitellus had not reached the necessary stage to impress upon the embryo the character of the maternal metabolism and with it the characteristic female features" (p. 16).

The cause of the concomitance of sex and particular somatic characters is believed by Russo "to depend upon a suitable modification of the germ-cell, related in some way to the age, the physiologic state and other conditions of the particular individual" (p. 98).

The evidence here appears unequivocal that external conditions (*e. g.*, nutrition) can determine the kind of sex and entirely vitiate the Mendelian scheme of ordinary crosses. Female sex and the maternal character of coat color moreover are shown to be associated with a more highly nourished egg, the artificially modified metabolism expressing itself in an abundance of deutoplasmic and chromatic substances (chromidial-net) in the zona pellucida and vitellus. The main stages in the chain of causes culminating in female sex seems to be, (*a*) high nutrition (lecithin), (*b*) increased size (preponderant anabolism), (*c*) storage of chromatin, (*d*) femaleness.[6]

A brief paper by Miss Boring[7] gives the results of a careful study of fertilized eggs of *Ascaris* with special reference to the

[6] The relation of nutrition to sex-determination as demonstrated by Russo for the rabbit suggests a possible physiologic basis for the theory of sex-causation in man (based solely on clinical facts) as recently advocated by Dawson to the effect that females develop from eggs from the left ovary and males from eggs from the right ovary;—namely, that the permanent passive congestion in the left ovary, due to the entrance of the left ovarian vein at a right angle into the renal vein (whereas the right ovarian vein empties obliquely directly in the inferior vena cava) may produce a condition of relatively better nutrition. Cognizance must be taken of the fact, however, that the right ovary is frequently slightly larger than the left, a point which apparently contradicts the verity of this interpretation; but cytological investigation may reveal a better nourished condition of all of the ova of the left ovary, expressed in the presence of chromidal nets, etc.

[7] Boring, Alice M., "A Small Chromosome in *Ascaris megalocephala*," *Arch. f. Zellforschung.*, Bd. 4, H. 1, 1909.

small odd chromosome previously noted by Herla and later also by Boveri. This peculiar chromosome is said to be very rare in the variety *bivalens*. Its representative was never discernible in the oögonia and only very rarely in the spermatogonia. From observations of bastard eggs the conclusion is drawn "that the small chromosome surely comes from the spermatozoön in some cases, and possibly from the egg in others" (p. 125—one instance noted). The possibility is suggested that the small chromosome is a sex-determining heterochromosome; but Miss Boring has no doubt also that it is sometimes due to fragmentation.

Boveri[8] inclines to regard this fifth ("X")—chromosome of *Ascaris megalocephala bivalens* (present in approximately half the eggs) as comparable to the accessory chromosome of *Pyrrhocoris*. He considers it more probable that its occasional apparent absence (common condition in *univalens*) is the result of fusion with one of the other chromosomes, than that its presence is the result of fragmentation. He concludes that the "x-chromosome" appears to be an independent structure specific for the male sex—as was originally believed by McClung for insects. In analogy with conditions in insects (*e. g., Protenor*), Boveri assumes a dimorphism of spermatozoa, due to the presence of the x-element in half of the sperm and its absence in the other half. But the unfertilized eggs are supposed to have no homologous elements (there being no evidence of such structures); hence, contrary to his recent generalization that the female fertilized egg contained the greater amount of chromatin, the male sex here seems conditioned by, or concomitant with, a relative preponderance of chromatin. This contradiction is elucidated by facts discovered by Boveri and Gulick (*op. cit.*, p. 136) in a study of the spermatogenesis and maturation of *Heterakis*, a nematode of the pheasant. The spermatogonial cells have 9 chromosomes; the maturation spindles of the eggs 5. Two types of spermatids are produced, one with 4 the other with 5 chromosomes; and one kind of egg with 5 chromosomes. The condition is identical with that described by Wilson for the hemipter, *Protenor*.

These facts established for *Heterakis*, give a clue to the more probable state of affairs in *Ascaris*. Boveri reconciles the discrepancies by assuming a close union in the oöcytes of the homologues of the accessory chromosome with the other chromosomes thus masking their presence. In reality, then, *Ascaris mega-*

[8] Boveri, Th., "Ueber 'Geschlechtschromosomen' bei Nematoden," *Arch. f. Zellforschung.*, Bd. 4, H. 1, 1909.

locephala bivalens would have six (6) chromosomes in the female and five (5) in the male (apparently four (4) in each since the heterochromosomes commonly couple with the ordinary chromosomes).

The attempt to rationalize the assumption of such a union involves the hypothesis of chromosome individuality in extreme form, viz: "We can not doubt that also in the apparently homogeneous nucleus of the spermium each chromosome preserves its individuality; but all are most closely pressed together" (p. 139). The greater effort here demanded (as compared with the egg pronucleus) to separate the chromosomes in this more compressed condition affects also the odd chromosome and frequently disjoins it from its "companion."

Thus two more forms (from the group of the Nematodes) are shown to conform to Wilson's scheme of sex-determination. And though Boveri is forced to retract (p. 137) his former statement regarding a preponderance of chromatin in the female sea-urchin as judged from Baltzer's plates the evidence accumulates that the female sex is somehow associated with a greater amount of chromatin.[9]

In an extensive paper of 110 pages on sex-determination in *Polyps,* Nussbaum[10] describes in detail a large series of experiments extending from 1891 to 1897 on *Hydra grisea.* His discussion of results involves comparisons with the works principally of Krapfenbauer (*H. fusca*), Frischholz (*H. fusca* and *H. grisea*), Whitney (*H. viridis*) and Annandale (*H. orientalis*).

The aquaria were all arranged under similar conditions of light and heat; only the nutritive conditions were caused to vary by changes in the amount of food supply and by induced periods of budding. The temperature is said to have an effect on sex only indirectly through influence on the nutrition. In contradistinction to the four above-named investigators, Nussbaum maintains that the nutrition and not the temperature is the chief factor which determines change from the asexual or budding condition to the sexual (diœcious and hermaphrodite); though he agrees with the latter two that for each species there is a definite temperature-optimum.

[9] The case of *Acholla multispinoa* described by Payne (*Biol. Bull.,* Vol. 16, nos. 3 and 4, 1909) may perhaps prove a real exception, though it may be harmonized, as Payne suggests, by assuming a greater combined activity for the several smaller "differential chromosomes," than for the single absolutely larger male member.

[10] Nussbaum, M., "Ueber Geschleschtsbildung bei Polypen," *Arch.* (*Pflüger*) *f. Physiologie,* Dec. 30, 1909, Bd. 130.

With good feeding budding gives place to a sexual phase. On the basis of daily observations of many cultures for a number of years Nussbaum concludes that a more favorable nutritive condition produces the female polyp. "The mass of food governs budding and the production of sexual organs"—and the best nutrition produces females. The same polyp may enter upon repeated sexual phases each separated by a period of budding; but, while he seems to deem it possible, he has not yet succeeded in changing the sex of the same individual polyp directly into the opposite sex.

Here again the same general conclusion appears that sex is consequent upon the degree of nutrition and that the best nourished polyp produces eggs, i. e., high nutrition conditions the female sex.

Nussbaum suggests an interesting new interpretation of hermaphroditism (gynandromorphism) among insects where a dimorphism of spermatozoa prevails, i. e., where heterochromosomes are found. He believes it quite possible that occasionally the reducing division may be omitted in spermatogenesis and that the unmatured spermatocytes may develop directly into functional sperm. Shortly before, or at the time of, the first segmentation of an egg fertilized by such a spermatozoon, the male pronucleus is supposed to undergo its belated reduction division, one half (with the even number of chromosomes) passing to one daughter cell with one half of the developing egg pronucleus, and the other half (with the odd number of chromosomes) with the other similar half to the other cell. Thus would result a two-cell stage, one blastomere (female) containing one more chromosome than the other blastomere (male). If then, as has been experimentally demonstrated in several forms, each blastomere gives rise to one half of the resulting individual the symmetry of the insect hermaphrodite would be explained. Here again sex is thought of as determined by a quantitative relation of chromatin.

The results of the newer investigations on sex-determination seem, at least temporarily, to have brought us back to the position of Geddes and Thomson, namely, that femaleness is causally related to a dominating cell-anabolism and maleness to a relatively preponderant cell-katabolism. This conclusion would seem to be the base from which future investigations will start in the attempt to further elucidate the fundamental mechanism of sex-differentiation.   H. E. JORDAN.

UNIVERSITY OF VIRGINIA.

RECENT INVESTIGATIONS ON THE COMPARATIVE ANATOMY OF CONIFERS

UNTIL quite recently there has been an increasing tendency to regard the two important coniferous tribes which are, at the present epoch, respectively characteristic of the northern and southern hemispheres, viz., the Abietineæ and Araucarineæ, as of different origin and not nearly allied with one another. This view of their derivation is, for example, represented by Professor Seward in his monograph on the Araucarineæ[1] and by Professor Penhallow in his "Manual of North American Gymnosperms."[2] A similar opinion has even quite recently been expressed by Mr. Thomson.[3] While the inferences of those whose conclusions are based almost entirely on a consideration of the structure of existing representatives of the Coniferales and of their surmised ancestors from the Paleozoic, have had the marked separatist trend indicated above, of late quite another tendency has made itself felt as a consequence of the structural investigation of the Mesozoic conifers and a comparison of these with existing tribes.

An important contribution on the structure of the Jurassic woods of King Karls Land[4] contains an account of a ligneous species, which the author names *Cedroxylon transiens*. This species is remarkable for the fact that it at the same time manifests the ray structure of the Abietineæ and in many instances the characteristic alternating radial pitting of the tracheids, which is a feature of the wood in existing Araucarineæ. On account of the latter feature Gothan, while referring the wood to the abietineous genus *Cedroxylon* Kraus, applies the specific appellation *transiens,* to indicate that in his opinion the wood in question marks a transition from the Abietineæ to the Auracarineæ. Of the general soundness of this view there can be no question. Nearly contemporaneously Jeffrey published an account of another Mesozoic wood presenting the same structural peculiarities as *Cedroxylon transiens,* together with the added abietineous feature of the possession of short or spur shoots, re-

[1] "The Araucarineæ, Recent and Extinct," *Phil. Trans. Roy. Soc. London,* 1906.

[2] Ginn & Co., Boston, 1907.

[3] "The Megasporophyll of *Saxgothea* and *Microcachrys*," *Bot. Gazette,* 47, May, 1909.

[4] Gothan, W., "Die Fossilen Hoelzer von Koenig Karls Land," *Kung. Svensk. Vetenskap. Handlingar,* 42, No. 10.

sembling in their anatomical relations those of the living *Pinus*.[5] The latter author, however, differs diametrically in his point of view from Gothan, since he regards *Araucariopitys,* in spite of its numerous abietineous features, as none the less an araucarian conifer and as indicating the derivation of the Araucarineæ from an abietineous ancestry rather than the reverse, as is assumed by Gothan.

Quite recently Hollick and Jeffrey have published an extensive memoir on the structural remains of the Cretaceous conifers of Staten Island,[6] in which they describe for the first time the anatomical organization of the branches, leaves and cones of a number of well-known Mesozoic conifers hitherto recognized from impressions alone. They reach the conclusion that the external appearance of Mesozoic conifers is in general very misleading as to their real affinities. The supposed Sequoias of the Cretaceous, for example, turn out from the internal examination of all their organs not to belong to the modern genus at all but to be closely related to those araucarian conifers, which are at present limited in their range to the southern hemisphere. The same result is reached in regard to a number of other genera, which have been connected with the living Sequoiineæ, Cupressineæ and even the Podocarpineæ. These authors further conclude that the general structure of Cretaceous conifers of araucarineous affinities is good evidence for the derivation of the Araucarineæ from a stock resembling the Abietineæ and not for the reverse mode of origin, which is universally accepted by those whose conclusions are mainly based on a structural and habital comparison of living conifers with the gymnosperms of the Paleozoic, since the transitional forms are all clearly on the araucarian side.

Sinnott has recently described an araucarian wood, which in the former state of our knowledge would have inevitably been referred to the abietineous genus *Cedroxylon* Kraus.[7] From the study of the ray structure of this fossil wood and from the examination of the tracheids in connection with new criteria recently formulated, this author comes to the conclusion that his wood represents a type of the Araucarineæ, transitional towards

[5] Jeffrey, E. C., "*Araucariopitys,* A New Genus of Araucarians," *Bot. Gazette,* Dec., 1907.

[6] "Cretaceous Coniferous Remains from Kreischerville, New York," *Mem. New York Bot. Garden,* III, May, 1909.

[7] Sinnott, E. W., "*Paracedroxylon,* A New Type of Araucarian Wood," *Rhodora,* Vol. II, Sept., 1909.

the ancestral Abietineæ, which he names *Paracedroxylon,* on account of its general resemblance to the abietineous wood genus *Cedroxylon* Kraus.

In an important though brief article on the occurrence of the "bars of Sanio" in recent and extinct coniferous woods, Miss Gerry[8] comes to the interesting conclusion that the presence of this structural feature, consisting of transverse bands of cellulose interposed between the radial pits of the tracheids of the wood, is characteristic of all conifers, *except the Araucarineæ.* Her results are of special significance in connection with the conclusions reached by Jeffrey and Hollick, cited above, in regard to the true affinities of the supposed Sequoias, Thuyas, etc., of the Mesozoic. On the basis of the absence of the bars of Sanio in well-preserved woods of supposed Cretaceous Sequoias, etc., she arrives at the result that these are in reality of araucarian affinities, as was inferred by the authors just mentioned, as the consequence of the combined structural study of the branches, leaves and cone-scales of the conifers in question.

The general result of all the investigations cited in the foregoing paragraphs is to show that there existed during the Mesozoic conifers, which were clearly transitional between the abietineous and araucarineous types of the present day. The predominance of the testimony moreover in favor of the Abietineæ rather than the Araucarineæ having been the older coniferous tribe is apparent. Recently Jeffrey has brought forward very definite positive evidence in favor of this view, based on the structure of Mesozoic pines.[9] Known structurally heretofore only as to their wood, the pines of the Cretaceous, which are not without closely allied relatives in the earlier Mesozoic, are here described in relations to the very important features of leaf structure. Among the abietineous remains the most significant because the most archaic genus is *Prepinus* Jeffrey, which has a detailed resemblance in foliar organization to certain Cordaitales of the Paleozoic, as well as the centripetally formed primary wood which is the common possession of the Pteridophyta and the lower gymnosperms. The author was moreover able to trace a complete seriation among various representatives of Cretaceous pines, in leaf organization, from the type presented by *Prepinus,* to that which characterizes contemporary species of *Pinus.* It thus appears that the abietineous line is definitely connected with the

[8] Gerry, Eloise, *Annals of Botany,* Vol. 24, No. 93, Jan., 1910.

[9] Jeffrey, E. C., " On the Structure of the Leaf in Cretaceous Pines," *Annals of Botany,* Vol. 22, No. 86, April, 1908.

Paleozoic gymnosperms, particularly with the Cordaitales, and in this respect has the strongest claim to be considered as the oldest representative of the coniferous stock.

In a recently published article, Jeffrey considers certain abietineous features, such as resin canals of the secondary wood, or the occurrence of marginal ray tracheids, which are found as abnormalities in certain species belonging to the sequoiineous and cupressineous tribes of conifers.[10] He reaches the conclusion that these abnormal abietineous features of the tribes in question are not indications of the derivation of the Abietineæ from them, as has been inferred by Penhallow and others, since recent structural paleobotanical investigations show that the Abietineæ are immeasurably older geologically than the sequoiineous or cupressineous tribes. The conclusion is arrived at that the resin canals or ray tracheids, which sporadically occur in the woods of *Sequoia, Thuya, Sciadopitys, Cunninghamia,* etc., indicate that the Sequoiineæ and Cupressineæ came off from the Abietineæ in the late Mesozoic or early Tertiary, after the latter had developed marginal ray tracheids in their wood rays.

The general result of numerous recent investigations on the anatomy of living and extinct conifers is to show that the two coniferous tribes which have to-day diametrical polar distribution are both very old, reaching back as far as the Paleozoic, that now widely separated geographically and anatomically they once flourished side by side in the northern hemisphere and were connected phylogenetically by a series of transitional forms. The preponderance of evidence moreover seems to vouch for the greater age of the Abietineæ. The more modern and cosmopolitan tribes, the Sequoiineæ, Cupressineæ, Taxineæ, and Podocarpineæ appear further to have been derived from abietineous forebears at a comparatively recent epoch. Even the Podocarpineæ of present characteristic antarctic range, appear from Miss Gerry's interesting investigations, to have come from the general abietineous stock and not from the Araucarineæ, as has been the conclusion of those who have recently investigated the microgametic structures of the araucarians and podocarps, since the latter possess bars of Sanio, which never occur in the Araucarineæ.

E. C. Jeffrey.

Harvard University.

[10] " Traumatic Ray-Tracheids in *Cunnighamia sinensis*," *Ann. Bot..* 22, No. 88, Oct., 1908.

PLATE I

THE SKELETON OF DIPLODOCUS CARNEGIEI, MOUNTED IN THE CARNEGIE MUSEUM, PITTSBURGH

THE LENGTH FROM THE TIP OF THE NOSE TO THE END OF THE TAIL OVER CURVES IS 84½ FEET; THE HEIGHT AT THE HIPS IS ABOUT 14 FEET. REPLICAS THUS MOUNTED ARE LOCATED IN BERLIN, PARIS, VIENNA AND BOLOGNA